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Diminution des ressources planctoniques et artificialisation de l'habitat : Quelles conséquences sur le fonctionnement des communautés aquatiques ?

Un aperçu via l'étude des niches écologiques des communautés de macroinvertébrés et de poissons de la Meuse belge et française

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Faculty of Sciences

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DIMINUTION DES RESSOURCES PLANCTONIQUES ET ARTIFICIALISATION DE L'HABITAT - QUELLES CONSÉQUENCES SUR LE FONCTIONNEMENT DES COMMUNAUTÉS AQUATIQUES?

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A dissertation submitted by

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in fulfillment of the requirements

for the degree of PhD in Biological Sciences.

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DIMINUTION DES RESSOURCES PLANCTONIQUES ET ARTIFICIALISATION DE L'HABITAT - QUELLES CONSÉQUENCES SUR LE FONCTIONNEMENT DES COMMUNAUTÉS AQUATIQUES?

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Par Adrien LATLI

RESUME

Si les effets des invasions biologiques sur la biodiversité ont été largement étudiés par la communauté scientifique, certaines de leurs implications peuvent être exacerbées notamment dans les écosystèmes fortement anthropisés. Depuis la fin du XX^{eme} siècle, un nombre croissant d'études témoigne de la diminution des ressources planctoniques des grands cours d'eau, tendance qui est souvent corrélée avec l'apparition de mollusques invasifs filtreurs. S'ensuivent généralement de multiples modifications dans la structure, la composition et le fonctionnement des communautés. Ces changements sont fréquemment soit exacerbés, soit confondus par diverses variables environnementales. Malgré l'importance de cette question dans la compréhension globale des écosystèmes, la contribution de la chenalisation des cours d'eau est rarement prise en compte comme facteur de stress lors d'études trophiques ou fonctionnelles.

L'objectif principal de cette thèse de doctorat est d'évaluer l'influence de la diminution des ressources planctoniques et du degré d'anthropisation hydromorphologique de la Meuse sur le fonctionnement des communautés de macroinvertébrés et de poissons de différents biefs de la rivière.

La première partie repose essentiellement sur une collection de base de données d'inventaires biologiques. Nous y démontrons que l'abondance du phytoplancton a diminué sur l'ensemble du linéaire de la Meuse étudiée, et a influencé le fonctionnement des communautés en entrainant une raréfaction des taxons se nourrissant dans la colonne d'eau au profit d'espèces benthivores. L'augmentation de l'abondance des poissons invertivores et du grand cormoran a significativement impacté les taxons de macroinvertébrés et de poissons de plus grande taille, à durée de vie plus longue et maturité sexuelle acquise à un âge plus élevé. En revanche, l'évolution temporelle des autres paramètres physico-chimiques ne semble pas influencer les traits d'histoire de vie des taxons constituant les communautés.

La seconde partie combine des données d'échantillonnages historiques et des inventaires biologiques récents. Nous y établissons que, suite à la diminution des ressources planctoniques, les biefs aménagés pour la navigation fluviale offrent une plus faible diversité de ressources basales que les biefs impropres à la batellerie, limitant potentiellement la niche

trophique des communautés de poissons et de macroinvertébrés. Toutefois, les analyses isotopiques révèlent que malgré le fait que la niche trophique des macroinvertébrés soit plus étendue sur le bief non navigable, les communautés de macroinvertébrés benthiques des deux sites consomment majoritairement des matières organiques provenant de la ripisylve ainsi que des végétaux aquatiques. Les ressources alternatives telles que le seston ainsi que le periphyton ne contribuent que très faiblement au réseau trophique.

La troisième partie porte essentiellement sur une évaluation de la niche trophique des jeunes poissons de l'année via une approche basée sur les isotopes stables. Nous tentons de confirmer qu'en cas de faible disponibilité des ressources planctoniques, la compétition trophique intra et inter-stades au cours du développement ontogénique des jeunes poissons est plus importante dans les biefs aménagés pour la navigation. On observe sur les deux stations que les alevins consomment une part plus importante de végétaux aquatiques que les juvéniles, malgré le faible intérêt énergétique de cette ressource. Cette compétition alimentaire semble être renforcée en Meuse navigable où la spécialisation alimentaire au sein de la population d'alevins est significativement plus marquée forçant une partie des individus à consommer des ressources peu énergétiques.

Les résultats obtenus soulignent l'influence de l'habitat dans le maintien de la diversité taxonomique et de la dynamique du système. La chenalisation des rivières et l'homogénéisation des habitats ont eu un effet particulièrement délétère sur le fonctionnement des communautés et sur la résilience des hydrosystèmes qui ne peut qu'être renforcé par les différentes activités humaines et les changements globaux.

PLANCTONIC RESOURCES DECREASE, AND HABITAT ALTERATIONS, WHICH CONSEQUENCES FOR THE FUNCTIONING OF COMMUNITIES?

An overview through the ecological niches of macroinvertebrates and fish communities of the Belgian and French River Meuse

by Adrien LATLI

ABSTRACT

Many large European rivers have undergone multiple pressures that have strongly impaired ecosystem functioning at different spatial and temporal scales. Global warming and human activities have favored the invasion of exotic species, deeply modifying the structure of aquatic communities in large rivers. In many rivers, exogenous species alter trophic interactions within assemblages by increasing the predation risk for potential prey species and limiting the dynamics of others via the limitation of resource availabilities. Effects of these alterations according to the degree of river channelization have been poorly investigated so far. Rivers laid out for navigation could be more sensitive to trophic perturbations due to a lower diversity of available resources and a stronger trophic redundancy within communities.

The main objective of this thesis was to evaluate the influence of planktonic resource decrease on the functioning of macroinvertebrates and fish communities in relation to the degree of hydromorphological anthropization of the River Meuse.

In the first part, we studied long-term combined effects of global warming, trophic resource decrease, predation risk, and water quality variations on the trait-based structure of macroinvertebrate and fish assemblages over 26 years and 427 km stretch of the River Meuse. The study of temporal variations in biological, physiological, and ecological traits of macroinvertebrates and fish allowed identifying community trends and distinguishing impacts of environmental perturbations from those induced by biological alterations. We provide evidence, for this large European river, of an increase in water temperature (close to 1 ° C) and a decrease in phytoplankton biomass (-85%), as well as independent effects of these changes on both invertebrate and fish communities. The reduction of trophic resources in the water column by invasive molluscs has dramatically affected the density of omnivorous fish in favor of invertebrate feeders, while scrapers became the major feeding guild among invertebrates. Macroinvertebrate and fish communities have shifted from large-sized organisms with low fecundity to prolific, small-sized organisms, with early maturity, as a response to increased predation pressure.

In the second part, we investigated the trophic niches of macroinvertebrate and fish communities from two differentially regulated reaches of the River Meuse, both affected by reduced water column resources. We hypothesized that the impact of the planktonic decrease should have been lower in the less regulated reach, regarding community indices. Firstly,

based on a trait-based approaches, we provide evidence that the potential trophic niches of the communities were affected at both sites by the phytoplankton decrease with a greater impact on the most altered site. In the less regulated reach, the functional equitability and the specialization increased in the trophic niches of the macroinvertebrate communities during the decrease of the planktonic resources while the indices stayed constant in the channelized reach. Secondly, based on stable isotope approaches, we highlighted that (i) the trophic niche was slightly smaller in the channelized sector, with a significant contribution of allochthonous detritus and bryophytes at both sites; and (ii) taxa in the most disturbed site had a lower trophic niche overlap between sympatric consumers.

In the third part, we quantified the trophic niches of three cyprinid species (common bleak *Alburnus alburnus*, chub *Squalius cephalus*, and roach *Rutilus rutilus*) and one percid species (European perch *Perca fluviatilis*) at various stages of development, in order to compare intra- and interspecific competitions between sites differing in their degree of channelization. Using stable isotope analysis in two reaches of the River Meuse differing by their degree of regulation, we hypothesized that habitat heterogeneity increased the trophic specialization at different life stages by offering more alternative resources which reduce food competition, notably during the early period of life. We provided evidence that, in the context of low planktonic biomass, most young-of-the-year relied on benthic food sources. Furthermore, the River Meuse flow and depth regulation significantlty impacted the abundance and species richness of young-of-the-year. In the heavily channelized reach, between-stages competition and low resource diversity increased the diet partition between cyprinid larvae and forced a part of individuals to consume non-optimal energetic food sources such as aquatic vegetation. On the other hand, in the less channelized reach, larvae displayed a generalist feeding habit focusing on energetic prey such as different taxa of macroinvertebrates, suggesting that the diversity of habitat reduces the food competition within and between stages and the predation risk.

This research took place within a multi-stressor context where it is complex and difficult to statistically explain the variation of a single dependent metric by a specific independent variable because of potential confounding effects. Nevertheless, the study highlighted (i) the importance of trophic relationships in community dynamics, (ii) the potential role of new exotic taxa in the trophic functioning of rivers, and (iii) the potential influence of channelization that can unbalance the trophic functioning, reducing the fish community diversity and magnifying trophic disturbances.

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La réalisation d'un doctorat est un processus long et complexe qui ne peut être l'œuvre d'un seul Homme. Ma famille, mes amis et mes collègues ont apporté une contribution essentielle à ce travail et je souhaite via ces quelques mots les remercier chaleureusement.

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Introduction

1. Les grandes rivières de plaine, des écosystèmes complexes sous pression

a. Description et fonctionnement écologique

Les écosystèmes d'eau douce ne représentent qu'une faible superficie de la surface de la terre (0,8%), mais cette petite fraction ne supporte pas moins de 100 000 espèces différentes, soit presque 6% de la biodiversité mondiale (Dudgeon *et al.*, 2006). Ces milieux ont été particulièrement altérés par les activités humaines, la dégradation des habitats, les altérations hydrologiques, la pollution et l'introduction d'espèces éxogènes, à tel point qu'on estime que 25% des espèces de poissons d'eau douce sont menacées d'extinction dans le monde (Vié *et al.*, 2009). L'étude des cours d'eau n'est pas chose aisée, car ce type de milieu offre une large diversité de morphologies, de ressources et de perturbations au sein d'un même bassin versant. Le flux d'eau unidirectionnel depuis l'amont du bassin versant vers l'aval est une caractéristique essentielle à prendre en compte pour la compréhension du fonctionnement de ces écosystèmes. Au fil du bassin versant, l'hydrologie, la morphologie, la physico-chimie et les ressources organiques évoluent, créant des biotopes spécifiques peuplés d'une grande diversité d'espèces adaptées à ces caractéristiques.

En règle générale, la tête du bassin versant de la rivière présente les caractéristiques suivantes : une forte pente et une vitesse de l'eau élevée, mais un faible débit et une largeur du lit mineur réduite. Les contraintes physiques façonnent le substrat de la rivière où seuls les minéraux de grande taille résistent au processus d'érosion. Plus en aval, la température de l'eau augmente et la réduction de la vitesse du courant permet la sédimentation progressive des éléments en suspension. Le débit et la largeur augmentent et la rivière tend à serpenter dans la plaine alluviale. La température de l'eau connait des variations saisonnières qui peuvent être importantes, entrainant des déficits ponctuels de l'oxygène dissous lors des périodes chaudes dans les milieux à forte biomasse végétale. Ce gradient physique longitudinal de l'amont vers l'aval du cours d'eau modifie les flux de matière organique et contraint les communautés végétales et animales à s'adapter aux caractéristiques du milieu et aux ressources alimentaires disponibles (Thorp *et al.*, 2008).

C'est à partir des années 1950 que les premières théories rapprochant les caractéristiques hydromorphologiques des rivières et les assemblages faunistiques ont été proposées. Marcel Huet a mis en avant les conséquences de la vitesse du courant et de la largeur du lit mineur dans la distribution des communautés piscicoles (Huet, 1962). Il a établi quatre zones théoriques liées au profil en long des cours d'eau d'une région biogéographique donnée, les parties les plus en amont seraient favorables aux salmonidés et à leurs espèces accompagnatrices du fait de la vitesse du courant, de la température peu élevée de l'eau et du faible ensoleillement. Les zones situées en aval seraient en revanche propices aux espèces

cyprinicoles plus adaptées aux eaux chaudes et lentiques. Cette théorie bien que relativement ancienne est de nos jours encore couramment consacrée dans les ouvrages généraux d'écologie des eaux douces du fait de son approche élémentaire et facilement observable. Néanmoins, de nombreux scientifiques ont approfondi ce concept en y intégrant de nouvelles variables descriptives liées aux caractéristiques de l'habitat ou aux ressources trophiques disponibles. En 1980, Vannote *et al.* proposent la théorie du « river continuum concept » (RCC) décrivant la répartition des communautés de macroinvertébrés benthiques et des flux de matières organiques le long du gradient longitudinal du cours d'eau. Cette théorie, suggère que la végétation riveraine (ou ripisylve) joue un rôle fondamental dans les réseaux trophiques dulcicoles. La ripisylve contrôle fortement la disponibilité de l'énergie lumineuse et chimique disponible dans le cours d'eau pour les zones les plus en amont car, du fait de la faible largeur de la rivière, la quantité de lumière atteignant le benthos est extrêmement faible. Cette matière organique grossière provenant du milieu terrestre (allochtone) représente la majorité de l'énergie disponible de par la faible production chlorophyllienne autochtone. Cette source d'énergie profite aux macroinvertébrés benthiques collecteurs et broyeurs qui consomment les micro-organismes se développant sur les feuilles et le bois morts. Dans les zones plus en aval, l'apport d'énergie lumineuse augmente avec l'élargissement du cours d'eau, ce qui profite aux végétaux aquatiques (periphyton, bryophytes, macrophytes). A cela s'ajoute la matière organique présente dans les particules fines dérivant de l'amont issues majoritairement de la fragmentation mécanique et de la dégradation par les micro-organismes et macro-organismes des éléments plus grossiers. Cette énergie autochtone remplace peu-à-peu la matière allochtone liée à la ripisylve. Les macroinvertébrés qui en profitent sont en majorité des herbivores qui raclent le substrat en quête des micro-organismes se développant dans le périphyton ou aspirent le contenu des cellules des végétaux (Wallace & Webster, 1996). Au fil de l'eau, la largeur du cours d'eau augmente et la profondeur alliée à la turbidité devient limitante pour le développement des macrophytes. L'énergie disponible provient alors essentiellement des matières en suspension dérivant ainsi que du phytoplancton. Les communautés des macroinvertébrés benthiques sont alors dominées par les organismes collecteurs et filtreurs.

Le RCC a toutefois été adapté en fonction du contexte hydrogéographique et des activités humaines (Petts & Amoros, 1996). De plus, de nombreux scientifiques ont proposé des théories parfois contradictoires, parfois complémentaires au RCC. La théorie du « River Habitat Templet » se distingue du RCC car elle est a considérer à l'échelle plus restreinte de l'habitat et relie l'organisation des communautés biologiques à l'hétérogénéité spatio-temporelle de l'habitat (Townsend & Hildrew, 1994). Elle suppose que les caractéristiques de l'habitat ont forgé les stratégies d'adaptation des organismes (en termes de survie et reproduction) qui ont developpé des traits d'histoire de vie spécifiques aux conditions environnementales correspondantes. Un environnement changeant au cours du temps sera préférentiellement peuplé par des espèces prolifiques, au cycle de vie court, de faible taille, mobiles et capables d'établir différentes formes de résistances. Un environnement plus stable

pourra accueillir, en plus des espèces décrites précédemment, des taxons de plus grande taille, moins prolifiques, peu mobiles et n'ayant pas développé de mécanismes de survie spécifique.

D'autres théories contestent le RCC, notamment sur l'origine de la matière organique majoritairement consommée dans les rivières de plaine. Selon le RCC, l'énergie disponible dans cette partie du cours d'eau provient essentiellement de la matière en suspension dérivant de l'amont et du phytoplancton. Toutefois, dans leur théorie du « Flood Pulse Concept », Junk et *al.* (1989) suggèrent que le RCC sous-estime la part des apports provenant du bassin versant et plus précisément, de la ripisylve, des annexes hydrauliques et du bassin versant. Le transport du carbone organique provenant de l'amont n'aurait qu'une faible incidence sur la productivité du système. Bien que le « Flood Pulse Concept » résulte d'études sur des écosystèmes fluviaux tropicaux, cette théorie a été adaptée aux cours d'eau tempérés par Thorp & Delong (1994). Le « Riverine Productivity Model » (RPM) estime que la matière organique provenant de l'amont, qu'elle soit dissoute ou particulaire, est difficile à assimiler pour les organismes. En revanche, la matière organique provenant de la ripisylve, une fois transformée par les micro-organismes, est plus assimilable et contribue largement à la productivité des systèmes aquatiques ainsi que les végétaux aquatiques (algues et spermaphytes) qui sont souvent, à tord, peu considérés lors des études trophiques (Thorp & Delong, 2002). Le RPM considère que les sources de carbone allochtone peuvent supporter une part plus ou moins importante de la productivité du système via la boucle microbienne et qu'ils sont à l'origine d'une grande partie de la diversité taxonomique rencontrée dans les cours d'eau (Figure 1).

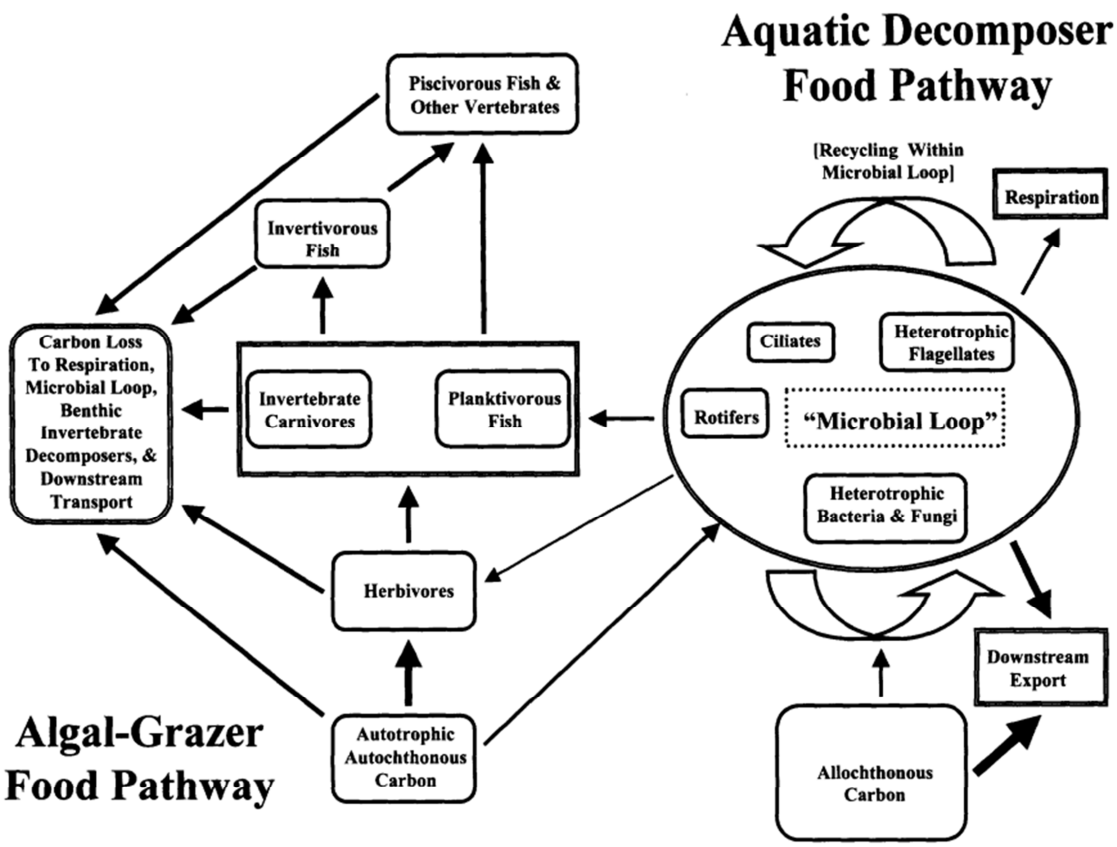


Figure 1: Illustration conceptuelle simplifiée d'un réseau trophique d'une rivière de plaine selon le RPM. Il existe deux voies énergétiques principales, via les algues planctoniques et benthiques, et via les organismes décomposeurs. La majorité de la biomasse des individus composant le réseau sont des organismes métazoaires de niveau trophique élevé, issus de la voie « algale ». Toutefois, une part importante du carbone utilisée par les algues provient de la boucle microbienne des décomposeurs. Les flèches représentent les transferts de carbone entre les compartiments du réseau trophique. Tirée de Thorp & Delong (2002).

Ces différentes théories ainsi que la variabilité dans les conclusions des études trophiques des milieux dulcicoles soulignent que la réalité est souvent plus complexe que le cadre théorique du RCC (Brett *et al.*, 2017) et que l'étude d'un cours d'eau nécessite souvent de considérer des interactions dépassant le cadre du lit mineur. De fait, nous avons rapporté au cours de ce chapitre une vision longitudinale ou transversale de l'hydrosystème, mais à notre connaissance ces concepts n'intégrent pas l'aspect vertical et, mésestiment souvent l'influence temporelle (Amoros *et al.*, 1988; Ward, 1989). Ce n'est qu'au début des années 2000 que ces aspects ont été mis en avant dans la synthèse globale des écosystèmes fluviaux (Riverine Ecosystem Synthesis) réalisée par Thorp *et al.* (2006a). Plutôt que de proposer un nouveau modèle, les auteurs mettent en évidence les multiples relations entre écologie et géomorphologie au sein de la mosaïque de patchs (ou habitat au sens du RHT) composant l'hydrosystème. La distribution spatio-temporelle de ces patchs ainsi que leur dynamique et les processus écologiques liés, déterminent la structure et le fonctionnement de l'écosystème. Cette vision complexe de l'écosystème fluvial, bien qu'étant très théorique, est actuellement

la plus complète et nous permettra dans la partie suivante de détailler les effets de certains perturbations anthropiques sur les différents grands domaines de l'hydrosystème.

b. La régulation des cours d'eau et ses conséquences écologiques

La plupart des rivières de plaine ont subi d'importantes modifications anthropiques au cours des siècles passés (Strayer *et al.*, 1999). La fertilité des plaines alluviales et la commodité de la navigation fluviale ont incité les Hommes à aménager fleuves et rivières pour leur propre usage. Afin de limiter les dégâts liés aux aléas hydrologiques, de nombreux aménagements hydromorphologiques ont été mis en place au cours du siècle dernier. L'édification de barrages et de mesures de protection des berges a des impacts directs ou indirects sur les caractéristiques hydromorphologiques des rivières. Les fleuves sont alors transformés en masses d'eau lentiques, au courant homogène tout au long de l'année hors période de crue (Poff *et al.*, 1997). L'habitat est également morcelé et homogénéisé (Poff & Schmidt, 2016) et les échanges entre les différents milieux (horizontaux) et les différents biefs (verticaux) sont également réduits (Roach *et al.*, 2009). Ces atteintes à l'intégrité des hydrosystèmes ont profondement modifié directement ou indirectement les communautés aquatiques, mais également le fonctionnement entier de l'écosystème. Les grandes rivières de plaine subissent une multitude de pressions globales et locales exercées directement sur le cours d'eau, depuis une zone plus en amont ou sur l'ensemble du bassin versant (Tockner *et al.*, 2010). Ces milieux sont donc fortement altérés par de multiples perturbations enchevêtrées les unes aux autres (Ormerod *et al.*, 2010) qui sont susceptibles d'évoluer au cours du temps et de l'espace (Heathwaite, 2010) en provoquant des réponses écologiques complexes (Davis *et al.*, 2010). La distinction et la quantification de chaque facteur de stress sur les communautés sont donc particulièrement difficiles à établir.

L'objectif de ce paragraphe n'est pas de lister l'intégralité des perturbations hydromorphologiques existantes mais de détailler les impacts potentiels de la régulation des grands cours d'eau de plaine sur les communautés aquatiques (principalement des macroinvertébrés benthiques et des poissons) par grands domaines de l'hydrosystème (hydrologique, géomorphologique et écologique, selon Thorp *et al.*, 2008).

Hydrologie

Les processus hydrologiques qui ont lieu au sein d'une rivière dépendent d'une combinaison de paramètres climatiques, topographiques et géologiques. Il est possible de caractériser l'hydrologie d'un cours d'eau via différentes variables (Tableau 1) telles que son débit moyen annuel et l'amplitude de ses variations, la fréquence et la durée des épisodes de hautes/basses eaux… Ces caractéristiques conditionnent l'intégrité écologique de l'hydrosystème tout entier (Poff *et al.*, 1997).

Tableau 1 : Exemples de perturbations anthropiques des hydrosystèmes d'ordre hydrologique. Tiré de Thorp *et al.* (2008).

Domain	*Attribute*	*Examples*
Hydrology		
	Magnitude	Reduction in peak flows, increased base flows, reduction or increase in mean annual flow
	Frequency	Increased occurrence of low-flow events, decrease in occurrence of smaller flow and flood pulses, increase in occurrence of mid-level flow events
	Duration	Prolonged low flows, reduction in length of overbank flows
	Timing	Seasonal reversal of flow events
	Rate of change	Increased rate of rise and fall of flow and flood pulses, increased stability of water levels
	Variability	Increases or decreases in flow events
	Predictability	Increased low-flow events, decreased events larger than flow pulses
	Patch character	Loss of abundance of hydraulic patches, redistribution of hydraulic patches

Une grande majorité des fleuves a été aménagée en vue de faciliter le transport fluvial. Ce type de modification anthropique perturbe les processus hydrologiques naturels en limitant les mouvements d'eau et de sédiments le long du cours d'eau. Les barrages modifient les variations de débit en créant des zones d'eaux lentiques, pouvant se réchauffer et s'évaporer fortement en période estivale et augmenter la sédimentation des particules en suspension (Zarfl *et al.*, 2014; Winemiller *et al.*, 2016).

Les processus hydrauliques et thermiques jouent un rôle fondamental dans les interactions biotiques et dans la croissance, la survie, le métabolisme et le comportement des organismes (Durance & Ormerod, 2007, 2009). De nombreux scientifiques ont rapporté que ces deux types de facteurs influencent la production primaire et les flux énergétiques (Descy & Gosselain, 1994; Floury *et al.*, 2012) mais également l'abondance et la diversité des communautés planctoniques (Elliott *et al.*, 2006; Descy *et al.*, 2012), des macroinvertébrés benthiques (Usseglio-Polatera & Beisel, 2002; Floury *et al.*, 2013; Latli *et al.*, 2017a), ichtyologiques (Buisson *et al.*, 2008; Buisson & Grenouillet, 2009; Pool *et al.*, 2017). Basées sur de longues séries de données temporelles, des études ont mis en évidence une corrélation entre les changements de structure et de composition des communautés en relation avec des évolutions hydrologiques et thermiques (Daufresne *et al.*, 2004; Daufresne & Boët, 2007; Durance & Ormerod, 2007; Vaughan & Ormerod, 2012). Des grandes rivières comme la Loire, le Rhône, la Meuse, l'Hudson ou le Mississippi (Fruget *et al.*, 2009; Roach *et al.*, 2009; Strayer *et al.*, 2011; Latli *et al.*, 2017a) ont vu leurs communautés évoluer, d'un assemblage spécifique dominé par les espèces rhéophiles affiliées aux rivières à vitesse de courant élevée et au substrat de grosse granulométrie, vers un assemblage composé majoritairement d'espèces limnophiles tolérant les températures élevées et les faibles concentrations en oxygène dissous (Tableau 2).

Tableau 2 : Evolutions temporelles estimées de 28 modalités de traits de macroinvertébrés benthiques en fonction de différentes tendances environnementales observées. Consulter Floury *et al.* (2017) pour plus d'informations.

Trait	Category	Prediction	Rationale
Maximum size	<5 mm	↗	Better resistance to increasing man-induced pressure (warming)
	10–20 mm	↘	Lower resistance to increasing man-induced pressure (warming)
	>40 mm	↗	Large sizes enabled by hydraulic constraints reduction (decreasing flow)
Life-cycle duration†	≤1 year	↘	Increasing habitat stability (discharge reduction)
Number of reproductive cycles†	<1 yr^{-1}	↘	Lower resistance to increasing man-induced pressure (warming effects exacerbated by discharge reduction)
Reproduction (sexual)‡	Ovoviviparity	↗	Better resistance to increasing man-induced pressure (e.g. increasing oxygen deficit due to warming)
	Clutches: free, endophytic or terrestrial	↗	Reduction of flow forces (reduction in embryonic mortality if free clutches) + expected increase in macrophyte development (due to phytoplankton limitation) + lower embryonic mortality under stressful conditions in aerial (terrestrial clutches) and wet (endophytic clutches) habitats
Dispersal†	Aquatic passive	↗	Dissemination facilitated by the reduction of flow forces ('voluntary' drift)
	Aquatic active	↗	Dissemination facilitated by the reduction of flow forces (swimming)
Respiration†	Gills	↘	Increasing oxygen deficit due to expected warming(organisms with gills are more sensitive to oxygen depletion)
	Aerial (plastron, spiracle)	↗	Increasing oxygen deficit due to expected warming (adaptive advantage – aerial respiration is not impaired)
Current velocity preferences	Null	↗	Discharge reduction
	Slow (<25 cm s^{-1})	↗	As above
	Moderate (25–50 cm s^{-1})	↘	As above
	Fast (>50 cm s^{-1})	↘	As above
Temperature	Cold (<15 °C)	↘	Expected warming
	Warm (>15 °C)	↗	As above
Food‡	Plant detritus >1 mm	↗	Expected increase in macrophyte development (phytoplankton limitation)
	Living macrophytes	↗	As above
	Living microinvertebrates*	↘	Expected decrease in zooplankton and benthic meiofauna (phytoplankton limitation)
Feeding habits	Deposit feeder*	↘	Expected decrease in particulate organic matter availability (eutrophication reduction)
	Shredder*	↗	Expected increase in relative proportion of coarse detritus (decrease in particulate organic matter)
	Scraper, grazer*	↗	Expected increase in biofilm development (phytoplankton limitation)
	Filter feeder*	↘	Phytoplankton limitation
	Piercer (plants or animals) + parasite	↗	Expected increase in macrophyte development (phytoplankton limitation) + discharge reduction
	Predator (carver, engulfer or swallower)	↗	Discharge reduction
Trophic status	Oligotrophic	↗	Phosphorus concentration decrease and eutrophication reduction
	Eutrophic	↘	As above

Géomorphologie

La prise en compte de l'hydrogéomorphologie d'un cours d'eau permet de considérer la structure physique (du lit majeur, des berges et du lit mineur) et le fonctionnement de l'écosystème fluvial (Tableau 3).

Tableau 3 : Exemples de perturbations anthropiques des hydrosystèmes d'ordre géomorphologique. Tiré de Thorp *et al.* (2008).

Domain	*Attribute*	*Examples*
Geomorphology		
Riverine landscape	Connectivity	Increases and decreases in the flow and sediment loads
Floodscape	Stability	Increased and decreased erosion of floodplain surfaces
	Connectivity	Decreased flow connections between floodscape and riverscape, increased groundwater connections
	Dimensions	Reduction in the active floodscape area
	Patch character	Simplification and fragmentation of floodscape
	Composition	Loss of functional sets and units associated with floodscapes
Riverscape	Dimensions	Increased and decreased capacity of the active riverscape, change in shape and complexity of riverscape
	Planform	Straightening of the river channel, reduction in the number of river channels
	Slope	Downcutting of river channel
	Bed	Aggradation and degradation of the river bed, armoring of river bed sediment
	Patch character	Loss of functional sets and units within the riverscape, change in composition of functional sets and functional units
	Stability	Increased and decreased stability of the riverscape

La distribution des espèces dans les hydrosystèmes est partiellement liée à la distribution d'habitats hérité des contraintes géologiques et modifiés par les forces hydrologiques, le climat et la végétation (Thorp et *al.*, 2008). La diversité, la stabilité et la connexion entre ces habitats sont des éléments essentiels dans le maintien de la biodiversité car ils permettent aux différents organismes d'y réaliser l'intégralité de leur cycle de vie. Par exemple, la perte d'une connexion longitudinale liée à la mise en place d'un barrage infranchissable à la faune piscicole peut nuire aux espèces migratrices potamotoques (Poff & Schmidt, 2016). Sur la rivière Illinois, l'interruption des connexions entre les bras morts et le lit majeur induit localement l'exctinction de certaines espèces de moules d'eau douce dont les larves glochidies (parasites des poissons) étaient en déficit d'hôtes dans certaines zones *(Tucker et al*., 1996).

La variation du niveau de l'eau et la durée des périodes de hautes eaux permettent le maintien de la végétation rivulaire et des forêts/prairies alluviales qui offrent divers services écologiques (Figure 2). Les variations de débit au cours de l'année entretiennent la diversité specifique de la végétation et remettent en suspension les fines particules recouvrant le substrat, augmentant la productivité benthique et recréant des zones de fraie pour la faune ichtyologique. Les crues majeures participent aux échanges de matières organiques entre le lit majeur et le lit mineur (Poff *et al.*, 1997).

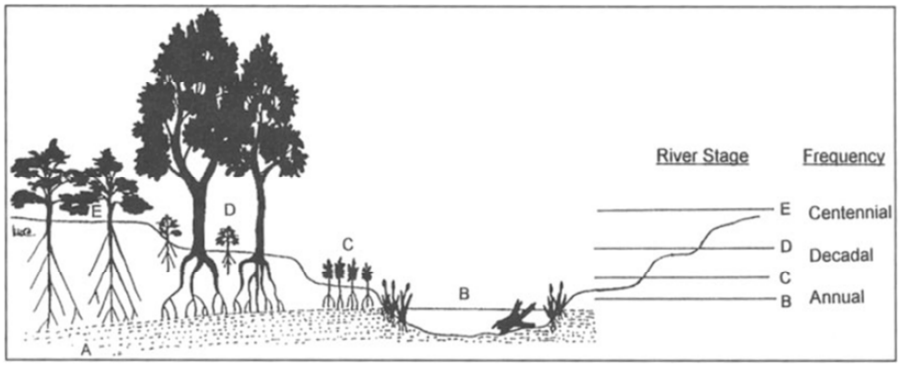


Figure 2: Coupe transversale d'un écosystème fluvial de plaine en fonction des aléas hydrologiques. Tirée de Poff *et al.* (1997).

Comme nous l'avons explicité précédement, la connexion "spatiale" entre les différents habitats joue un rôle prépondérant dans le fonctionnement de l'écosystème mais la composante "temporelle" est également à considérer. La magnitude ainsi que la durée des épisodes de hautes eaux diversifient les ressources exploitables et accroissent les productivités primaire et secondaire des écosystèmes aquatiques ainsi que l'abondance des invertébrés et des vertébrés (Jenkins & Boulton, 2003).

Depuis la prise de conscience écologique et la mise en place de travaux de renaturation des cours d'eau, de nombreux auteurs ont cherché à évaluer l'impact de différents types de restauration de la qualité physique de l'habitat sur les communautés de macroinvertébrés benthiques et de poissons (Lamouroux *et al.*, 2015). Il a été démontré sur le Rhône que la

reconnexion du lit mineur à la plaine alluviale couplée avec l'augmentation des débits réservés augmentait l'abondance des espèces de poissons lotiques lithophiles d'un facteur de 1,9 à 2,4 (Daufresne *et al.*, 2015; Lamouroux & Olivier, 2015). Castella *et al.* (2015) ont démontré que la diversité taxonomique des macroinvertébrés etait corrélée avec le degré de connexion latérale des rivières de plaine, la diversité granulométrique du substrat, l'abondance de la végétation aquatique et de la matière organique en décompostion. Certains taxons comme les trichoptères et certains éphémeroptères réagissent positivement aux travaux de renaturation de cours d'eau. La restauration des débits et des habitats diversifie les traits liés à la locomotion des organismes, aux régimes alimentaires et favorisent les espèces de large taille, à long cycle de vie avec une maturité sexuelle tardive (Mérigoux *et al.*, 2015).

Ecologie

La complexité des relations trophiques observées dans les cours d'eau de plaine dépend de l'abondance et de la diversité des espèces présentes et des ressources disponibles (Tableau 4). Ces facteurs sont partiellement dépendants de la géomorphologie du biotope, de l'hétérogénéité de l'habitat et de sa stabilité (Thorp *et al.*, 2008).

Tableau 4 : Exemples de perturbations anthropiques des hydrosystèmes sur les processus écologiques. Tiré de Thorp *et al.* (2008).

Domain	*Attribute*	*Examples*
Ecology		
	Competition	Introduction of nonnative species and changes in community composition
	Food resources	Shifts in importance or benthic or pelagic resources, altered primary productivity, changes in catchment and riparian inputs, changes in food quality
	Predation	Introduction of nonnative species, changes in community competition
	Reproduction and dispersal	Loss of reproductive and nursery habitats, disruption of migratory pathways

Certains scientifiques ont constaté que la morphologie du lit mineur influençait les caractéristiques du seston et de la matière organique ainsi que celles de ses consommateurs comme les macroinvertébrés benthiques (Walters *et al.*, 2007). Une autre étude suggère que la morphologie du lit mineur ainsi que l'évolution temporelle des débits peuvent conduire à l'exclusion de prédateurs (Doyle, 2006). Suite à la disparition du prédateur, l'abondance des proies augmente impactant la disponibilité des ressources basales (ressources primaires constituant la base du réseau trophique). Sur la rivière Eel, l'abondance des prédateurs décline lors des années où le débit de la rivière est plus faible que la moyenne. Les consommateurs primaires limitent alors le développement algal, mais lors des années à pluviométrie élevée, le recouvrement des algues est beaucoup plus important (Marks *et al.*, 2000). Une étude de Fry (2002) met en relation l'impact de la diminution de la connectivité entre le lit mineur et le lit majeur de la rivière Mississippi avec la diversité des ressources utilisées par les invertébrés benthiques et les poissons à différents stades de développement. La diminution de la connectivité latérale induit une diminution de la diversité du régime alimentaire et la complexité du réseau trophique.

Ces différents exemples laissent percevoir l'importance de l'hétérogénéité de l'habitat dans la diversité spécifique, la prédation, le stockage et le transport de la matière organique ainsi que la production autotrophe (Post & Takimoto, 2007). Toutefois, la géomorphologie n'explique pas l'entièreté des perturbations observées sur les communautés dulcicoles. L'introduction de certaines espèces, prédatrices ou ingénieures, peuvent avoir de sérieuses conséquences sur l'ensemble de niveaux d'organisation écologique (Simberloff *et al.*, 2013). Via des interactions directes (compétition trophique, prédation,…) ou indirectes (modification de l'habitat, nouveaux pathogènes,…), les espèces exogènes modifient la structure des communautés indigènes en terme d'abondance et de diversité spécifique. L'apparition d'une nouvelle interaction sur les niveaux inférieurs d'organisation biologique se répercute souvent aux niveaux supérieurs, impactant ainsi le fonctionnement de l'écosystème tout entier (Cucherousset & Olden, 2011; Strayer, 2012). En cas de prolifération, certaines espèces ingénieures peuvent en peu de temps réduire certains types de ressources, restructurer complétement le réseau trophique (Zanden & Casselman, 1999) et forcer les espèces concurrentes à des changements de régime alimentaire (Thomsen *et al.*, 2014). Suite à l'invasion de mollusques éxogènes (*Dreissena polymorpha* et *Corbicula sp.*), les grands lacs et rivières américains ont vu en quelques années les populations de bivalves natives décroître (Strayer *et al.*, 2008; Lercari & Bergamino, 2011). Les scientifiques ont également constaté des perturbations sur l'ensemble de la biocénose des bactéries présentes dans le sédiment (Frischer *et al.*, 2000) jusqu'aux poissons piscivores (Daniel *et al.*, 2005; Ward & Ricciardi, 2007a). Il a été rapporté que les caractéristiques environnementales étaient corrélées au succès d'une invasion. Les écosystèmes perturbés aux habitats homogènes, à la diversité spécifique faible et limités en nombre d'interactions biotiques sont particulièrement sujets aux invasions biologiques (Ricciardi & Macisaac, 2010).

2. Le concept de niche écologique

a. Histoire et définition

La compréhension du rôle de la biodiversité et de la dynamique des échanges d'énergie et de matière au sein de l'écosystème est un des objectifs majeurs des études écologiques. De par leurs activités, les organismes régulent de nombreux processus écologiques et augmentent la résilience de l'écosystème face aux variations environnementales. En 1917 Joseph Grinnell introduit une étude originale décrivant la réponse d'une espèce, le Moqueur de Californie (*Toxostoma redivivum*) vis-à-vis de certaines variables de son environnement. Cette vision dite *grinnellienne* décrit la niche d'une espèce comme un ensemble de facteurs environnementaux nécessaires à la survie et à la reproduction de ses populations. Dix années plus tard (1927), Charles Elton introduit sa vision du concept de niche centrée sur les interactions entre les espèces vivant un même biotope. La niche *eltonienne* ne prend donc pas en compte les facteurs environnementaux, mais le positionnement d'une espèce dans son réseau ainsi que son rôle et son effet sur les autres organismes. En 1957 George Evelyn

Hutchinson revisite le concept de niche et définit la niche écologique d'un organisme comme un volume dans un espace multidimensionnel dont les axes représentent des facteurs environnementaux (abiotiques et biotiques) permettant la croissance et la survie de l'espèce.

On distingue deux sortes de niche, l'une théorique (*niche fondamentale*) et l'autre déduite d'observations *in situ* (*niche réalisée* ; Figure 3). La niche *fondamentale* reprend l'ensemble des conditions abiotiques nécessaire à l'établissement d'une population. La niche réalisée, plus restrictive, ajoute l'effet des interactions biotiques dans la description (Devictor *et al.*, 2010).

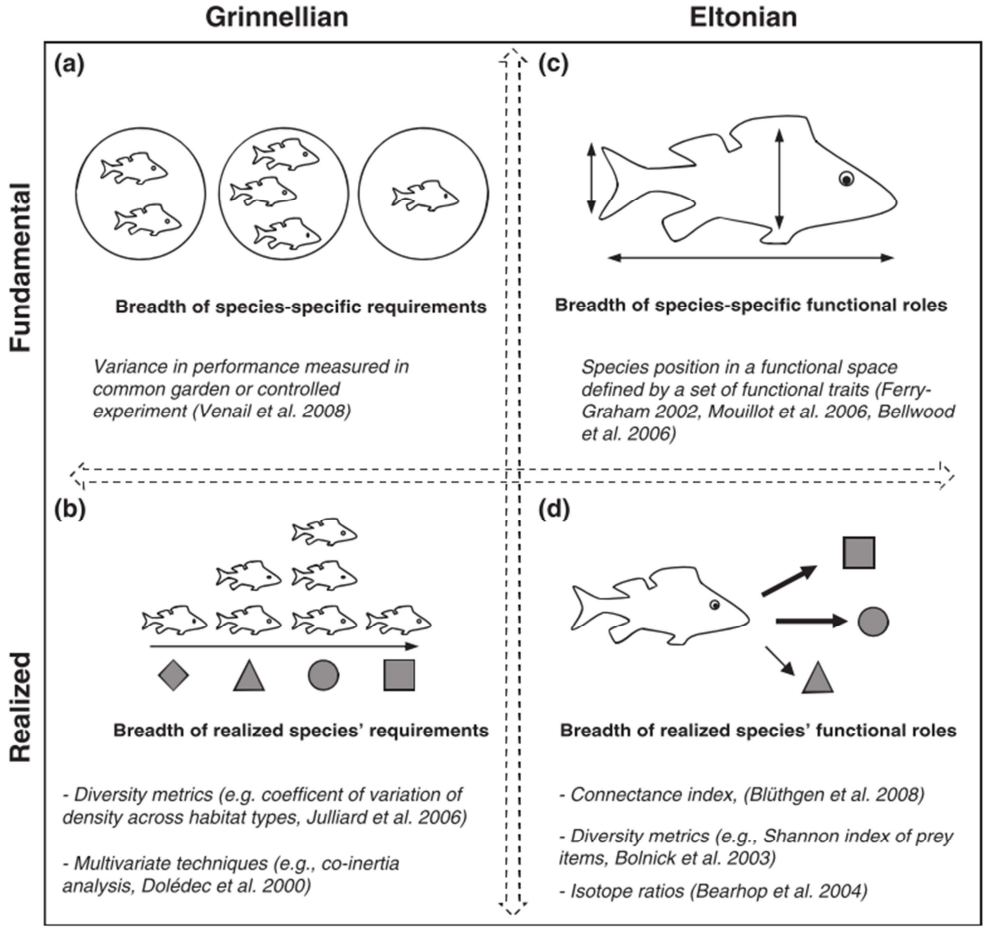


Figure 3 : Représentation des différents types de niches considérées (*grinnellienne* vs *eltonienne* – *fondamentale* vs *réalisée*). La figure représente (a) l'abondance d'une espèce dans un milieu contrôlé, (b) l'abondance d'une espèce selon l'habitat (symbolisé en gris), (c) le *fitness* d'une espèce selon ses caractéristiques biologiques, (d) l'impact de l'espèce sur d'autres espèces ou ressources (symbolisées en gris). Tirée de Devictor *et al.* (2010).

De nos jours, l'approche *grinnellienne* est principalement utilisée dans le domaine de la biogéographie afin de définir l'évolution des aires de répartition des espèces dans un contexte de changement climatique (Elith *et al.*, 2006). L'approche *eltonienne*, quant à elle, est particulièrement utilisée à l'échelle de la communauté lors d'études fonctionnelles basées sur les caractéristiques (physiologiques, morphologiques…) des taxons (Maire *et al.*, 2015) ou à

des niveaux très variables (de la communauté à l'individu) lors d'études trophiques (Newsome *et al.*, 2007).

La représentation des niches d'une espèce ou d'une communauté n'est qu'une caricature de la réalité qui reste très complexe à étudier du fait de la multitude des interactions biotiques ou abiotiques (stochastiques ou non). De plus la vision de la niche peut évoluer en fonction de l'échelle spatio-temporelle ou du domaine d'étude à laquelle elle est rattachée (Chase & Myers, 2011).

b. La niche trophique

Les relations trophiques jouent un rôle primordial dans le fonctionnement global de l'écosystème (Lindeman, 1942). Le fonctionnement de l'écosystème peut être appréhendé en décryptant les flux d'énergie entre les différents organismes ainsi que leurs interactions trophiques. C'est pourquoi la niche trophique, sous-ensemble de la niche écologique, a bénéficié d'une attention particulière de la part des biologistes. On peut considérer la niche trophique comme les ressources intégrées par un consommateur (niche trophique réalisée) ou comme les ressources potentiellement utilisables par les consommateurs en fonction de leurs caractéristiques phénotypiques (niche trophique fondamentale). Afin d'augmenter sa lisibilité, la niche trophique est généralement représentée en deux dimensions (Figure 4). La dimension verticale correspond généralement au niveau trophique de l'individu ou du taxon et la dimension horizontale représente l'affinité des individus/taxons à un certain type de ressource qui permet aisément de distinguer les consommateurs (Duffy *et al.*, 2007).

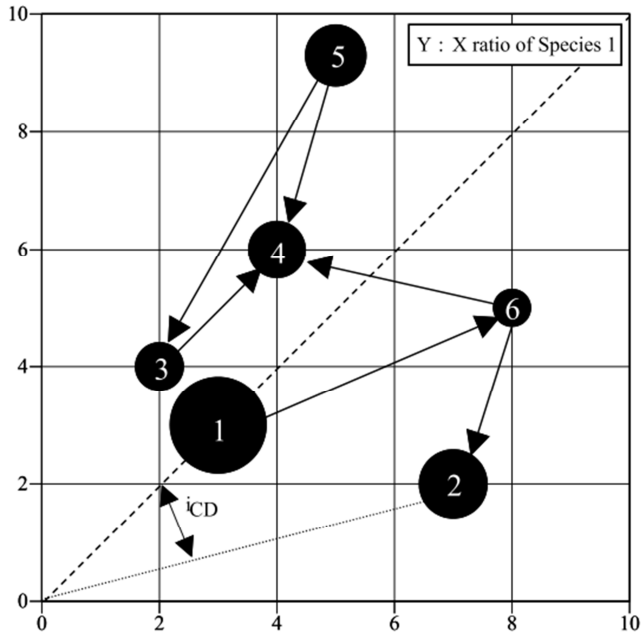


Figure 4 : Représentation théorique de la niche trophique de 6 espèces. Les axes X et Y peuvent être les quantités d'éléments chimiques, ou les axes principaux d'un espace fonctionnel. La largeur du

cercle noir correspond à la largeur de la niche trophique ou à l'abondance d'une espèce donnée. Les flèches noires indiquent les liens trophiques entre les espèces. Tirée de Woodward & Hildrew, (2002).

The angle between the dashed and dotted lines iCD represents the angular imbalance between species 1 and 2.

La modélisation des niches trophiques dans un espace bivarié est particulièrement utile pour caractériser les changements qui ont lieu au sein de la communauté ou de la population suite à une perturbation abiotique et/ou biotique de l'écosystème (Pakeman, 2011). En partitionnant l'effet des différents types de perturbations, il est possible de visualiser l'influence de chaque type de pression sur la niche trophique de la communauté ou de la population (Mouillot *et al.*, 2013). De nombreux facteurs environnementaux peuvent influencer la niche trophique car ils régulent partiellement la disponibilité des ressources. Il a été démontré par exemple que la fragmentation de l'habitat (Figure 5) a un impact significatif sur la taille de la niche trophique (Layman *et al.*, 2007a). Les populations de prédateurs évoluant dans un habitat peu diversifié ont ainsi un choix de proies potentielles plus faible, ils sont donc très dépendants d'un certain type de proies dont l'abondance peut varier au cours du temps et ainsi impacter significativement la compétition entre les consommateurs.

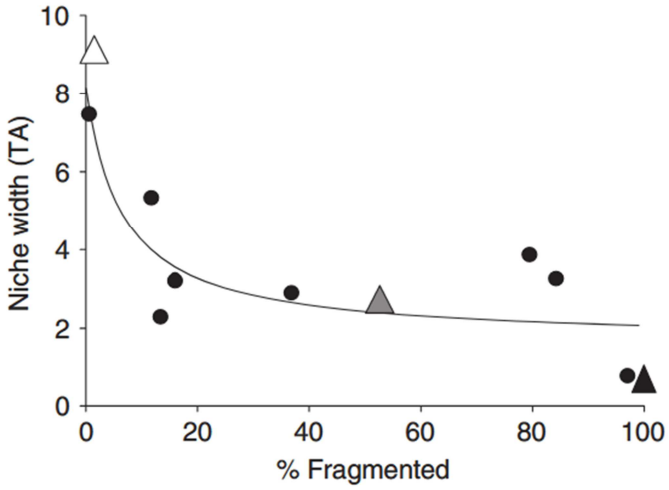


Figure 5 : Taille de la niche trophique (TA) de la Sarde grise (*Lutjanus griseus*) en fonction du pourcentage de fragmentation de l'habitat. Les triangles correspondent à la taille de la niche des Sardes échantillonées dans les différents habitats de références. Tirée de Layman *et al*., (2007).

De nombreux mécanismes biotiques peuvent également influencer directement ou indirectement la niche trophique d'une communauté, et peuvent conduire à des changements drastiques du régime alimentaire et/ou de l'abondance des individus (Rosemond *et al.*, 2000; Layman *et al.*, 2007a; Carpenter *et al.*, 2011; Estes *et al.*, 2011). De nombreuses publications ont mis en évidence les effets d'une modification de la structure verticale (top-down) et/ou horizontale (bottom-up) du réseau trophique a un effet sur le fonctionnement de l'écosystème, via un effet direct sur les consommateurs/proies mais également un effet indirect sur la

dynamique du cycle des nutriments (Askey *et al.*, 2007; Dineen & Robertson, 2010; Schmitz *et al.*, 2010; Estes *et al.*, 2011; Ruhí *et al.*, 2016; Suraci *et al.*, 2016).

c. Les interactions trophiques

Dans l'étude des différents types de relations biotiques influençant la structure trophique d'une communauté, trois principes sont considérés comme fondamentaux : la prédation, la compétition trophique et la spécialisation alimentaire (McCann *et al.*, 1998; Pawar *et al.*, 2012).

Via une interaction verticale « top-down », les prédateurs structurent les communautés animales, contrôlent l'abondance des proies et induisent des modifications morphologiques, physiologiques et comportementales sur ces dernières (Hawlena & Schmitz, 2010). La prédation joue un rôle essentiel dans le réseau trophique à tel point que la disparition d'un grand prédateur peut entrainer une cascade trophique qui modifiera profondemment l'écosystème tout entier (Estes *et al.*, 2011).

Pour le prédateur, l'acquisition de nourriture est un élément-clé qui doit être optimisé afin d'augmenter la survie et la compétitivité. Selon l'Optimal Foraging Theory (OFT; Charnov, 1976), chaque individu sélectionne ses proies afin d'optimiser le gain d'énergie en limitant le coût d'acquisition et en maximisant les bénéfices énergétiques fournis par la ressource. La balance énergétique dépend donc des caractéristiques de la proie, de la capacité du prédateur à capturer et assimiler la ressource et des risques liés à son acquisition. Les prédateurs consomment donc, dans un premier temps, les proies les plus profitables qui tendent à se raréfier, ce qui, à terme, augmente la compétition alimentaire et peut forcer à une diversification du régime alimentaire.

La compétition structure les populations et les communautés, dans lesquelles la nature et la force des interactions sont généralement déterminées par la taille, le stade de développement ou l'âge des organismes (Woodward & Hildrew, 2002b; Woodward *et al.*, 2005). Une population structurée, par stade de développement ontogénique par exemple, présentera deux types d'interactions compétitives, l'une au sein d'un stade donné (compétition intra-classe) et l'autre entre les différents stades (compétition inter-classes ; Araújo *et al.*, 2011). La compétition alimentaire peut être plus rude pour les individus d'une classe donnée vis-à-vis d'une autre classe en fonction de leur morphologie, leur physiologie, leur génétique, leur traits d'histoire de vie respectifs (Quevedo *et al.*, 2009; Dall *et al.*, 2012; Pauls *et al.*, 2013; Bouwhuis *et al.*, 2014; Biro & Sampson, 2015). Par exemple, chez les cyprins d'eau douce, les larves en post-résorption de la vésicule vitelline sont moins efficaces que les juvéniles pour capturer certains types de proies particulièrement profitables comme le zooplancton, car le faible développement des nageoires réduit leur mobilité et l'ouverture limitée de leur bouche les contraint à ne consommer que des organismes de faible taille et moins nutritifs, comme le phytoplancton (Nunn *et al.*, 2012).

La compétition trophique induit une croissance densité-dépendante, car une abondance de prédateur induit une forte compétition qui réduit l'abondance des proies et donc l'apport énergétique pour les consommateurs. En cas de surexploitation de la ressource nutritive, le degré de généralisme intra-classe des consommateurs a tendance à augmenter (dimension horizontale), sans que cette diversification du régime alimentaire ne touche tous les individus (Svanback & Bolnick, 2007). Certains individus, dont les capacités à se reproduire dans un environnement donné sont les plus élevées (ou *fitness* ; Hunt & Hodgeson, 2010), sélectionneront les proies les plus profitables tandis que les autres ajouteront de nouvelles ressources à leur régime alimentaire (Bolnick *et al.*, 2003). Cette variabilité trophique intra-spécifique, également appelée spécialisation individuelle (SI), correspond à une différenciation de la niche trophique des individus d'une même espèce (ou population) à travers les différentes proies consommées. La spécialisation individuelle (SI) de la population augmentera si les individus consomment des ressources différentes. Au contraire, si les individus convergent vers le même type de proie secondaire, la SI diminuera (Bolnick *et al.*, 2002).

Les effets potentiels des différents mécanismes écologiques comme la prédation, l'abondance des proies et/ou des consommateurs influençant la SI sont repris dans la Figure 6.

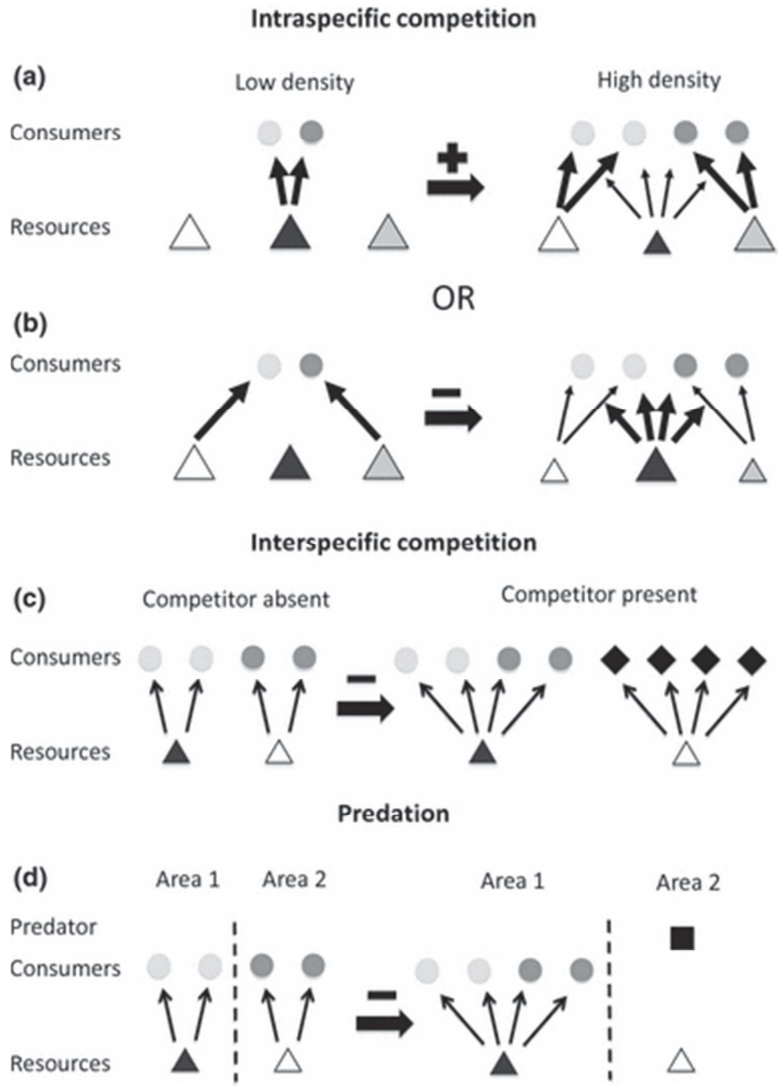


Figure 6 : Illustration de l'influence des mécanismes écologiques sur le degré de spécialisation individuelle. La taille de la flèche verticale indique la contribution de la ressource au régime alimentaire du consommateur. Les flèches horizontales illustrent l'influence du facteur étudié (positif ou négatif) sur la valeur de la SI. (a) A faible densité, les consommateurs aux phénotypes différents (niveau de gris) partagent la même ressource, la plus profitable (triangle gris foncé). Si le nombre de consommateurs augmente, l'abondance de la ressource la plus intéressante diminue forçant les individus à diversifier leur régime alimentaire (augmentation de la SI). (b) Autre possibilité, si les consommateurs ont chacun une ressource préférée, alors le régime alimentaire des 2 phénotypes est bien distinct en cas d'abondance des ressources. Mais si l'abondance des consommateurs augmente, les ressources les plus profitables vont diminuer obligeant les consommateurs des deux phénotyes à consommer complémentairement la même ressource non exploitée précédemment car moins énergétique (diminution de la SI). (c) En absence d'autres espèces compétitrices (losange noir), les consommateurs de différents phénotypes consomment différentes ressources (SI élevée). En présence de compétiteurs, un type de ressource peut ne plus être accessible aux consommateurs, qui doivent se contenter d'un type de ressource (réduction de la SI). L'inverse de la concurrence inter-spécifique est l'opportunité écologique, qui peut augmenter en raison de la diminution de la compétition et devrait avoir un effet positif sur la SI. (d) En cas de ressource affiliée à un type de microhabitat présentant un

risque de prédation élevé, la présence du prédateur (carré noir) peut réduire la SI des consommateurs. Araújo *et al.*, 2011.

L'intégration de la SI offre une vision plus complète des relations trophiques et de l'effet des changements de structure et de fonctionnalité des populations/communautés sur le fonctionnement de l'écosystème. Dans ce contexte, les jeunes cyprins de l'année sont un modèle biologique particulièrement intéressant puisque, en fonction de leur stade de développement, les individus sont très sensibles à la compétition trophique intra et inter-classe(s) (Nunn *et al.*, 2007a). De plus, ces poissons évoluent dans des environnements différemment perturbés, ce qui permet d'étudier l'influence de certains types de pressions anthropiques sur les interactions trophiques.

3. Méthode de description de la niche trophique

a. La niche fonctionnelle

L'étude des relations entre la biocénose et son environnement était habituellement considérée via une approche centrée sur les taxons/espèces. Cependant, de nombreux scientifiques ont révélé que le changement de la richesse spécifique ne joue pas un rôle prépondérant dans les processus fonctionnels qui régissent la communauté (Reiss *et al.*, 2009). Bien que certaines espèces-clés peuvent contrôler le fonctionnement de l'écosystème, via par exemple l'utilisation des ressources, il est possible qu'au sein de la communauté plusieurs taxons aient un rôle écologique identique (Walker, 1992; Loreau *et al.*, 2001). La disparition d'une espèce n'implique donc pas forcément un changement du fonctionnement écologique du système, car une autre espèce, indigène ou éxogène, peut potentiellement se subtituer à elle. Cette « redondance fonctionnelle » est en grande partie déterminée par les caractéristiques biologiques (morphologie, régime alimentaire…), physiologiques et écologiques des taxons concernés (Griffin *et al.*, 2009). La compréhension du fonctionnement d'un écosystème est donc concevable par l'étude de la niche fonctionnelle des organismes s'y développant, via une approche centrée sur les traits d'histoire de vie (Mouillot *et al.*, 2013). Les traits d'histoire de vie sont une description des traits fonctionnels, ou caractéristiques phénotypiques, qui déterminent la *fitness* d'un individu (Violle *et al.*, 2007). La niche fonctionnelle d'une communauté est représentée par un espace multi-dimensionnel dont les axes correspondent à l'utilisation des traits fonctionnels (Figure 7) dont les valeurs sont modulées par l'abondance des individus des différents taxons.

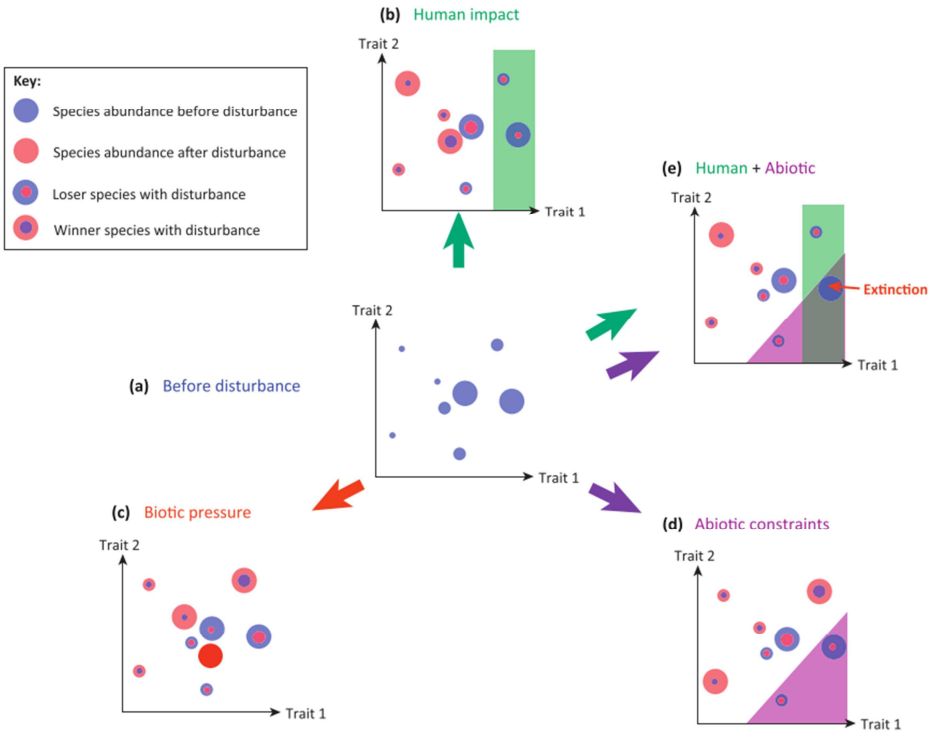


Figure 7 : Représentation théorique de la niche fonctionnelle d'une communauté en fonction de 3 types de pressions différentes. (a) Espace fonctionnel défini par 2 traits avec 8 espèces. (b) Effet anthropique fort pour les espèces ayant une affinité élevée pour le trait 1 (c) Effet potentiel de la présence d'un taxon exogène (cercle rouge), effet négatif sur les espèces compétitrices mais positive sur les prédateurs. (d) Contrainte environnementale élevée pour les taxons ayant une forte affinité pour le trait 1 et faible pour le trait 2. (e) combinaison des conditions (b) et (d) conduisant à l'extinction d'une espèce. Mouillot *et al.*, 2013.

La modélisation de la niche fonctionnelle d'une communauté repose sur la réalisation par codage flou (Chevenet *et al.*, 1994) d'une matrice reprenant l'affinité de chaque taxon vis-à-vis d'une combinaison sélectionnée de traits fonctionnels. Ces scores d'affinités sont croisés à l'abondance des individus des différents taxons constituant la communauté. A l'aide d'une analyse multivariée réduisant le nombre de dimensions, un espace bivarié est créé, permettant de visualiser l'espace fonctionnel de la communauté et de caractériser la niche fonctionnelle de la communauté via certaines métriques (Figure 8) proposées par Villéger et *al.* (2008) :

- La richesse fonctionnelle (FRic) considère le volume de la niche de la communauté dans l'espace fonctionnel. Un grand volume indique une importante diversification des caractéristiques fonctionnelles de la communauté,
- L'équitabilité fonctionnelle (FEve) apprécie la régularité des distances entre les différents taxons dans l'espace fonctionnel pondérée par l'abondance des individus de chaque espèce. Cet indice diminue lorsqu'un grand nombre d'individus ont des caractéristiques fonctionnelles identiques,
- La spécialisation fonctionnelle (FSpe) évalue la distance moyenne entre les différentes espèces et le centre de la niche pondérée par l'abondance des individus de

chaque espèce. L'indice diminue lorsque de nombreuses espèces se retrouvent proches du centre de la niche.

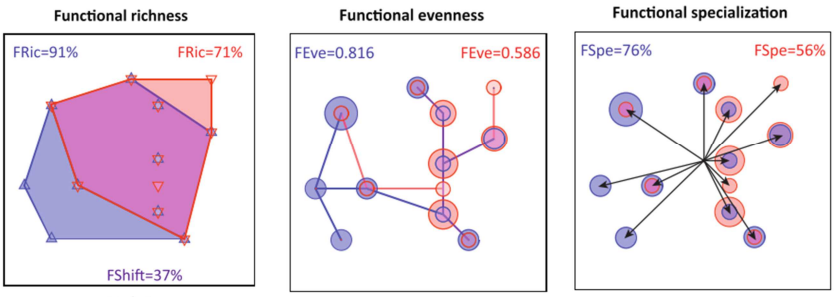


Figure 8 : Evolution potentielle de la niche fonctionnelle d'une communauté après perturbation (rouge). Les espèces sont représentées dans un espace bi-dimensionnel en fonction de leur affinité pour différents traits fonctionnels et de leur abondance relative.

Pour cette étude nous avons sélectionné deux bases de données de traits d'histoire de vie des macroinvertébré benthiques et des poissons publiées respectivement par Tachet et *al.* (2010) et Blanck et *al.* (2007). Ces bases de données permettent d'observer précisément les réponses des communautés à différents types de pression abiotique ou biotique (Dolédec & Statzner, 2008), à des échelles spatio-temporelles variées (Statzner *et al.*, 2001), d'établir un gradient des perturbations (Statzner *et al.*, 2004). La base de données utilisée comporte 9 traits biologiques et 10 traits écologiques décrits par 113 modalités pour les macroinvertébrés (c.f. chapitre 1, annexe S1) et 36 modalités rassemblées en 11 traits pour la faune piscicole (c.f. chapitre 1, annexe S2).

b. La niche isotopique

Suite à la démocratisation des analyses des isotopes stables dans le monde de la recherche, l'approche isotopique est devenue un standard dans l'étude de la structure des niches et des réseaux trophiques (Newsome *et al.*, 2007). Le terme « niche isotopique » est désormais employé pour décrire la niche trophique d'une population à partir des rapports isotopiques de deux éléments au minimum, généralement le carbone et l'azote (Vanderklift & Ponsard, 2003).

La technique des isotopes stables repose sur le fait qu'un même élément chimique (${}_{Z}^{A}X$), avec un nombre de protons bien défini (Z), peut avoir un nombre de neutrons variable. L'ajout d'un ou plusieurs neutrons rend l'élément plus « lourd » que sa forme standard dite « légère » (Fry, 2006). Les isotopes « lourds » sont généralement moins abondants dans le milieu naturel; *e.g.* l'isotope léger du carbone (^{12}C) représente 98,89% du stock global de carbon contre 1,11% pour le ^{13}C. De manière similaire, seulement 0,36% du stock d'azote global est composé de l'isotope lourd (^{15}N). Les variations des abondances isotopiques étant très faibles, les compositions isotopiques des échantillons sont donc comparées à des références internationales (V-PDB pour le carbone et l'azote atmosphérique pour l'azote) et exprimées en valeurs relatives (δ) et en ‰.

Malgré leur différence de masse, qui dépend du nombre de neutrons constituant l'élément, les isotopes participent aux mêmes réactions chimiques. Toutefois, la vitesse de réaction et les concentrations à l'équilibre thermodynamique varient en fonction de la masse de l'isotope, dite « légère » ou « lourde ». Lors de processus physiques ou biochimiques, les composés « lourds » présentent une plus forte énergie de dissociation vis-à-vis de l'isotope « léger » réduisant leur mobilité et augmentant leur accumulation dans les composées plus stables. Les molécules « légères » ont en revanche tendance à se recombiner plus rapidement (Fry, 2006). Ce fractionnement thermodynamique est le point essentiel de l'utilisation des isotopes en écologie trophique, car il permet de modéliser les échanges entre compartiments organiques et/ou inorganiques.

DeNiro & Epstein (1977 & 1978) ont évalué le fractionnement des isotopes de carbone et d'azote dans les relations trophiques. Ils ont découvert que, pour le carbone, l'enrichissement en isotope lourd lors d'une transition trophique proie-prédateur est négligeable (0,8+/-1,1‰) mais qu'il est en revanche un très bon marqueur de la source de carbone inorganique utilisé lors de la photosynthèse. En milieu aquatique, les molécules de CO_2 nécessaires à la photosynthèse des végétaux sont disponibles sous forme dissoute ; ces molécules sont enrichies en isotopes « lourds » par rapport au carbone atmosphérique. Il est donc possible de distinguer l'origine des matières carbonées présentes dans le milieu étudié (Figure 9).

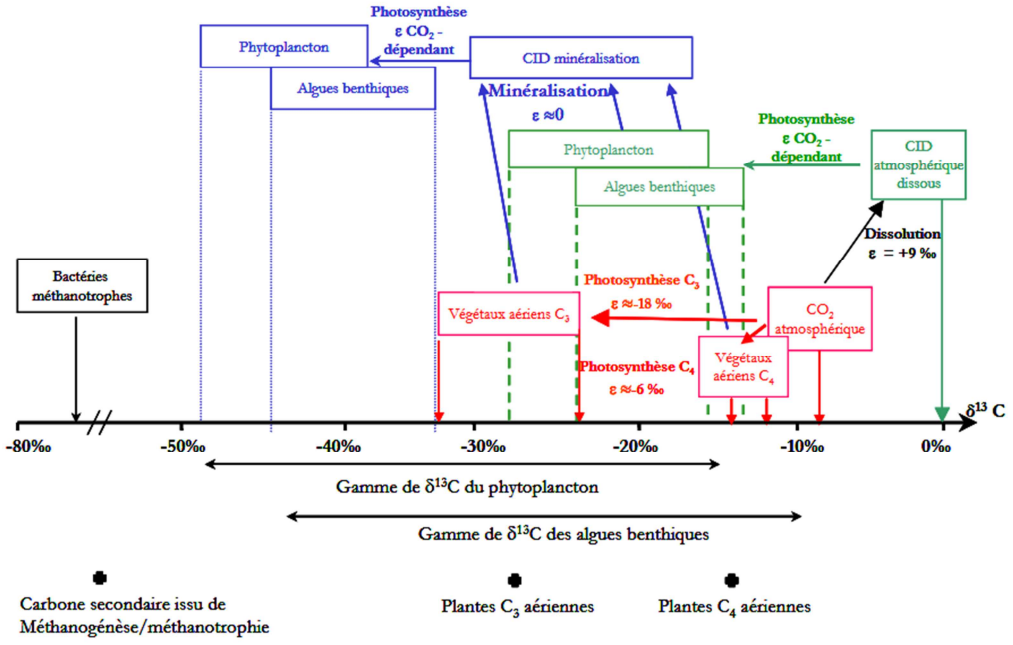


Figure 9 : Gamme de variations du $\delta^{13}C$ des producteurs primaires en milieu lacustre. Perga, *2007.*

En écologie trophique, l'analyse de l'isotope de l'azote ($\delta^{15}N$) est complémentaire à celle du carbone, car il est un marqueur pertinent de la relation proie-prédateur. Les consommateurs affichent un enrichissement en ^{15}N relativement similaire à chaque pas du réseau trophique, évalué à 3,4 +/-1,1‰ par Minagawa & Wada, (1984). Cet enrichissement est majoritairement dû à l'excrétion d'urine appauvrie en ^{15}N par le consommateur. D'autres études plus récentes

(Post, 2002a; McCutchan *et al.*, 2003) estiment l'enrichissement trophique moyen à 2,0 +/- 1,8‰. Le fractionnement étant variable en fonction du type de taxon, de son environnement et du tissu étudié, Caut *et al.* (2009) ont proposé une estimation des facteurs de fractionnement basée sur une compilation de 66 études (Figure 10).

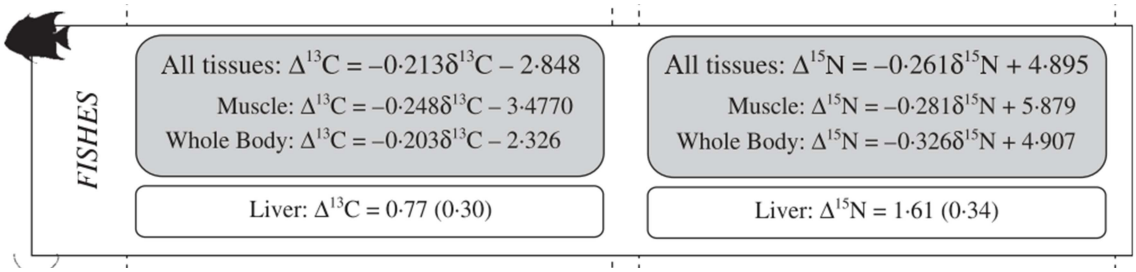


Figure 10 : Equations permettant de calculer le taux de fractionnement de $\delta^{15}N$ et $\delta^{13}C$ d'organismes vertébrés exothermes en fonction du tissu échantillonné. Tirée de Caut *et al.,* 2009.

Les valeurs isotopiques en $\delta^{13}C$ et $\delta^{15}N$ projetées dans un espace bivarié (Figure 11.a) permettent de visualiser la niche isotopique d'une population ou d'une communauté. L'ordonnée ($\delta^{15}N$) permet de distinguer le niveau trophique des consommateurs tandis que l'abscisse ($\delta^{13}C$) sépare les consommateurs en fonction des ressources primaires qui les composent. La projection de la distance maximale entre les consommateurs sur l'axe des X (CR ou $\delta^{13}C$ Range) est un indicateur de la diversité des ressources basales présentes dans l'écosystème consommées par la communauté/population étudiée. Son équivalent sur l'axe des Y (NR ou $\delta^{15}N$ Range) décrit la longueur de la chaîne trophique de la communauté (Figure 11.b). La surface englobant les valeurs isotopiques de tous les taxons composant la communauté peut être interprétée comme la niche trophique de la communauté (Figure 11.b). De la même manière qu'avec la niche fonctionnelle, il existe différentes métriques évaluant la distance moyenne entre les taxons et le centroïde de la communauté (CD ; Figure 11.c), ainsi que la distance moyenne avec le plus proche voisin (NND ; Figure 11.d ; Layman *et al.*, 2007). Les interactions au sein de la niche trophique peuvent être étudiées en fonction de la répartition des points dans la niche isotopique (Figures 11.c et 11.d) mais également entre deux ou plusieurs niches (Figure 11.e). Le recouvrement des niches isotopiques (ou *overlap*) est un indicateur de la compétition trophique qui peut être testé statistiquement à l'aide de modèles bayesiens (Layman *et al.*, 2012).

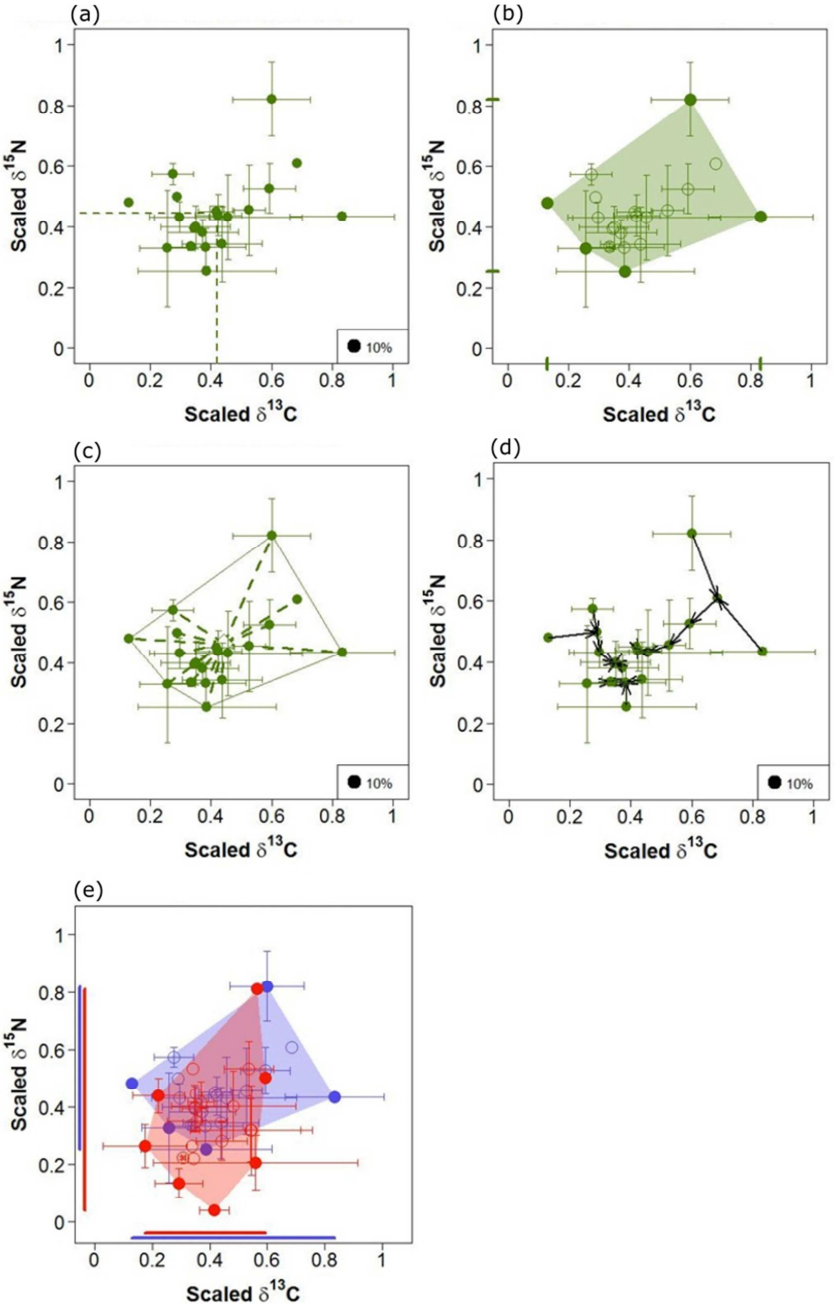


Figure 11 : Visualisation de la niche isotopique d'une (a:d) ou de deux communautés (e) de macroinvertébrés de la Meuse. Chaque point correspond à la valeur isotopique moyenne d'un taxon, les barres, verticale et horizontale, représentent la variabililité isotopique individuelle (SD).

c. Composante intraspécifique de la niche trophique

Au sein de la niche trophique d'une population, les individus consomment différemment les ressources alimentaires (Bolnick *et al.*, 2003), en fonction des ressources disponibles, du type d'habitat et de la pression de prédation (c.f. §2.c). De nombreux auteurs estiment qu'il est essentiel de prendre en compte ce type de variabilité du fait de son importance dans le maintien de la diversité fonctionnelle des populations et de sa relation avec les facteurs environnementaux et biotiques (Svanback & Bolnick, 2007; Araújo *et al.*, 2011; Bolnick *et al.*, 2011; Dall *et al.*, 2012). A une echelle spatio-temporelle plus large, la différenciation intraspécifique de la niche peut avoir des conséquences délétères sur la coexistence entre taxons (Hart *et al.*, 2016).

La variabilité intraspécifique trophique peut être considérée à l'aide d'une estimation du régime alimentaire (analyses isotopiques, contenus stomacaux…), ou de l'étude des traits biologiques d'une population. Les différences morphologiques entre individus peuvent refléter l'efficacité de capture de certaines ressources. Ce phénomène de « polymorphisme de ressources » (Smith & Skulason, 1996) est largement associé à des divergences d'utilisation d'habitats, liées à une ségregation spatiale pouvant conduire à une spécialisation individuelle. Ce phénomène a été mis en évidence en milieu lacustre dans lequel certaines espèces de poissons se répartissent le long d'un gradient pélagique-littoral (Malmquist, 1992; Harrod *et al.*, 2010; Matthews *et al.*, 2010). Les individus se nourrissant en zone pélagique ont généralement un corps allongé permettant une nage plus rapide corrélée à la capture de proies plus mobiles. En zone littorale, la forme du corps des consommateurs est plus « trapue », facilitant la manoeuvrabilité en habitat plus complexe (Smith & Skulason, 1996).

Les corrélations entre morphologie et régime alimentaire requièrent une certaine stabilité temporelle de l'habitat et des ressources (Bolnick *et al.*, 2003) comme en milieu lacustre, ce qui n'est pas le cas des milieux d'eau vive trop changeants au cours du temps. Il est alors communément accepté d'utiliser une estimation de la SI à l'aide d'une approche centrée sur les ressources alimentaires ingérées ou assimilées (Araújo *et al.*, 2007; Rosenblatt *et al.*, 2015; Bond *et al.*, 2016).

Bolnick *et al.* (2002) ont proposé une approche originale de mesure de la spécialisation alimentaire individuelle inspirée de la méthode de segmentation des niches proposée par Roughgarden (1972). La largeur totale de la niche trophique de la population (TNW ou Total Niche Width) qui équivaut à la diversité des ressources consommées par la population peut être divisée en deux parties (Figure 12) : la variation des ressources utilisées par chaque individu (WIC ou Within-Individual Component) et la variance entre les différents individus (BIC ou Between-Individual Component). Le ratio moyen entre la diversité des ressources utilisées par chaque individu (WIC) et la niche de la population (TNW) mesure le degré de SI au sein de la population. Une valeur proche de zéro indique que tous les individus de la population consomment plus ou moins les mêmes ressources (Figure 12.A). En revanche, une

valeur proche de 1 signifie que la spécialisation alimentaire est très élevée entre les différents individus qui composent la population (Figure 12.B).

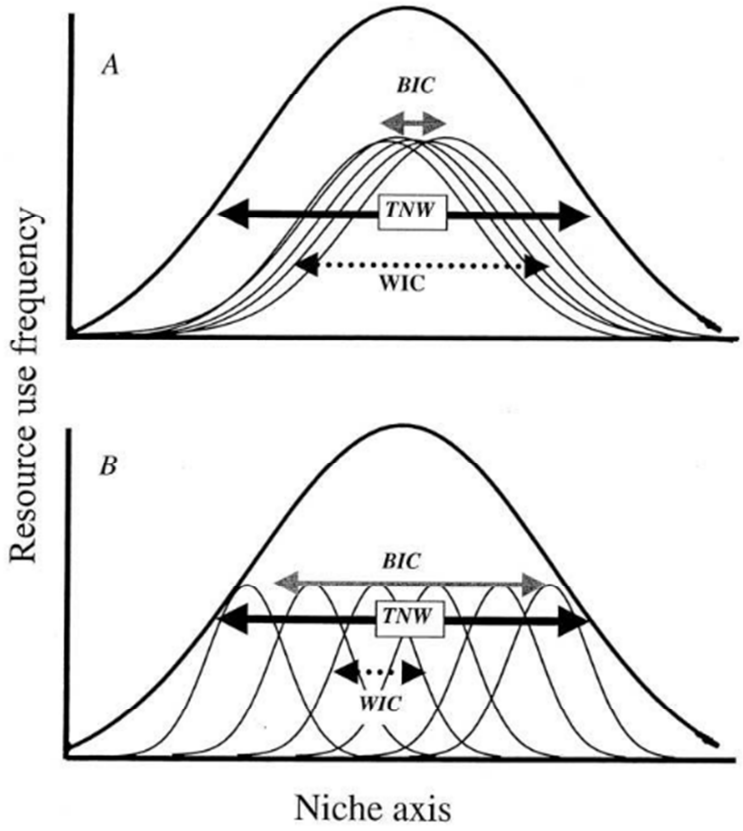


Figure 12 : présentation schématique de deux populations consommant les mêmes ressources mais réparties différement entre les individus. La courbe noire correspond à la niche totale de la population (TNW). Les courbes grises représentent la largeur de la niche alimentaire des différents individus composant la population (WIC). Le BIC estime la variance moyenne des ressources utilisées entre les différents individus. Pour une population généraliste (A), les différents individus consomment les mêmes ressources. En revanche si la SI augmente (B), les individus de la population consomment des ressources différentes de leur voisin. Bolnick *et al., 2003.*

Problématique de la thèse

1. Objectifs

L'objectif principal de cette thèse de doctorat est d'évaluer l'influence de la diminution des ressources planctoniques et du degré d'anthropisation hydromorphologique de la Meuse sur le fonctionnement des communautés de macroinvertébrés et de poissons de différents biefs de la rivière.

Dans une première partie, reposant essentiellement sur une collection de bases de données biologiques, nous étudions l'évolution temporelle de l'abondance du phytoplancton sur un long linéaire de la Meuse belge et française, ainsi que l'influence de la diminution des ressources planctoniques sur le fonctionnement des communautés de macroinvertébrés et de poissons. Nous émettons également l'hypothèse que l'évolution temporelle des autres paramètres physico-chimiques n'impacte pas significativement les traits d'histoire de vie des individus constituant les communautés.

Dans une seconde partie, en combinant les données d'échantillonnages historiques et les inventaires biologiques récents, nous enquêtons sur les conséquences de la diminution des ressources planctoniques sur la niche fonctionnelle des communautés de poissons et de macroinvertébrés en fonction des caractéristiques de l'habitat. Nous émettons l'hypothèse que les biefs aménagés pour la navigation fluviale offrent une plus faible diversité de ressources basales que les biefs impropres à la batellerie réduisant la niche trophique des communautés.

Dans la troisième partie, basée sur une approche ciblée sur les jeunes poissons de l'année, nous émettons l'hypothèse qu'en cas de faible disponibilité des ressources planctoniques, la compétition trophique intra et inter-stade(s) de développement ontogénique des jeunes poissons est plus importante dans les biefs aménagés pour la navigation.

2. Choix du site étudié : la Meuse, un fleuve hétéroclite

a. Description générale

La Meuse est un fleuve du nord-ouest de l'Europe (Figure 13) qui, malgré un linéaire relativement court de 925 km, traverse 3 pays et qui possède un bassin versant de 36 011 km² (Descy *et al*. dans Tockner *et al.*, 2009). Le bassin mosan est densément peuplé (environ 9 millions d'habitants en 2009) et les activités agricoles et industrielles y jouent encore un rôle important, même si les pollutions industrielles ont fortement diminué au cours des dernières décennies. Par contre, l'eutrophisation de la rivière est toujours bien présente. La pollution par des matières organiques biodégradables tend à diminuer depuis les années 1990, suite à la mise en place systématique de stations d'épuration des eaux usées. Toutefois, la qualité physico-chimique de l'eau et des sédiments est encore fortement impactée dans certains biefs

de la Meuse, notamment en aval de la confluence entre la Meuse et la Sambre (Commission internationale de la Meuse, 2011, 2015).

Figure 13 : Cartographie de la Meuse et des principaux sites d'échantillonnage utilisés lors de cette étude.

Pendant les années 1980 et 1990, les concentrations élevées en matières azotées et phosphorées ont favorisé la croissance du phytoplancton. Descy *et al*. (1994) ont constaté qu'en période estivale la concentration en chlorophylle-a dans la Meuse pouvait excéder 100 µg/L et que la communauté planctonique jouait un rôle essentiel dans la production de matière carbonée dans l'écosystème (Descy *et al.*, 2002). Cependant au cours des années 2000, l'abondance du phytoplancton a diminué à tel point que les concentrations de chlorophylle-a

mesurées en 2010 ne représentaient plus que 15% de celles mesurées dans les années 90 (Figure 14).

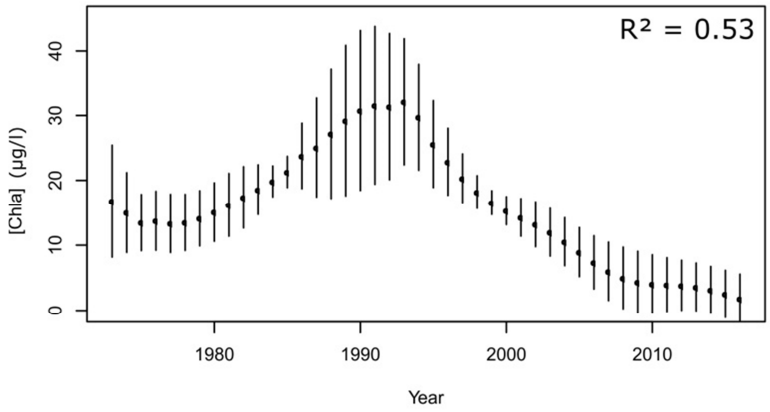


Figure 14 : Modélisation de l'évolution moyenne annuelle de la concentration en chlorophylle-a constatée sur 6 sites de la Meuse entre Saint-Mihiel et Eijsden depuis 1971.

Cette diminution du phytoplancton a également impacté les communautés de zooplancton de la Meuse. Dans les années 90, pendant toute la période estivale, les densités moyennes de zooplancton constatées étaient généralement comprises entre 300 et 500 individus L^{-1} avec des pics de densités proches des 4000 ind. L^{-1} (Viroux, 2002). Vingt ans plus tard, les densités mesurées en Meuse belge sont cent fois moindres et leur plage de distribution pendant la période de production est beaucoup plus réduite. Cette décroissance est particulièrement importante pour les rotifères, bien que ce groupe taxonomique ait été le plus représenté dans les années 90, les densités maximales post-2010 n'exèdant plus les 100 ind. L^{-1} (Figure 15).

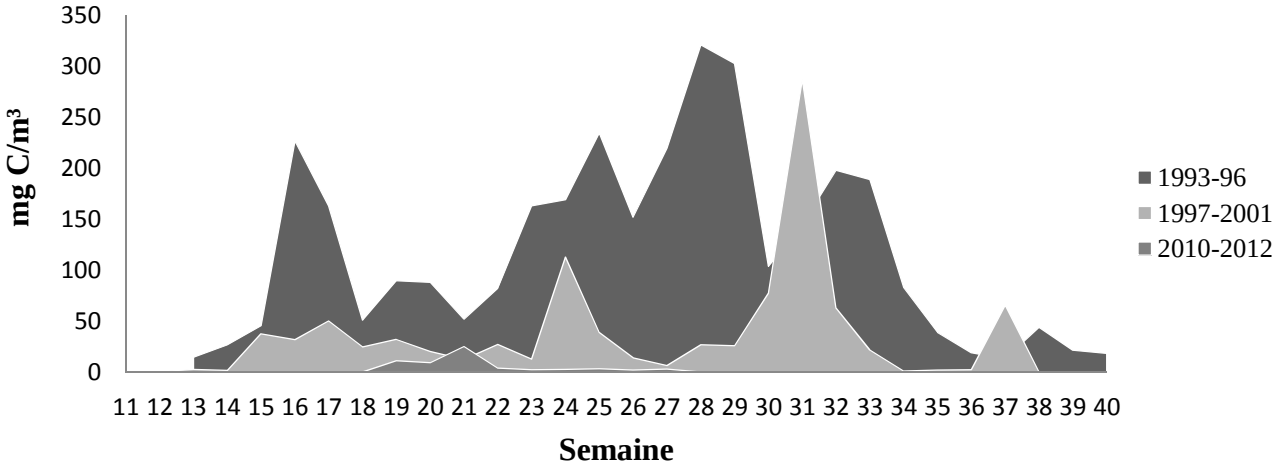


Figure 15 : Comparaison inter-annuelle de l'évolution des biomasses de rotifères à La Plante au cours de 3 périodes distinctes (1993-1996, 1997-2001, 2010-2012). Source des données : Viroux L.

Bien que les concentrations en matières azotées et phosphorées aient diminué pendant les années 90 suite au retraitement des eaux usées domestiques, ces nutriments restent en quantité suffisante pour ne pas limiter le développement du phytoplancton de la Meuse (Descy *et al.*

2009). Pigneur *et al.* (2014) ont démontré que la réduction des biomasses de plancton était principalement due à l'apparition d'un mollusque filtreur invasif, la corbicule (*Corbicula sp.*). Depuis son introduction en Meuse au cours des années 90, ce mollusque benthique a colonisé plus de 600 km de linéaire de la Meuse avec des densités maximales observées en Wallonie de plus de 700 ind. m^{-2} (données personnelles). Deux autres espèces de mollusques invasifs sont également bien représentées en Meuse, la moule zébrée (*Dreissena polymorpha*) et la moule quagga (*Dreissena rostriformis bugensis*), cette dernière étant arrivée plus tardivement dans l'écosystème Meuse. Lors du chômage technique de 2012, nous avons réalisé un inventaire des mollusques présents en Meuse avec une méthodologie similaire à celle réalisée par Libois et Hallet-Libois en 1983 (Tableau 5). En 29 ans, les densités de mollusques filtreurs ont été multipliées par plus de 100 avec une proportion de taxons invasifs de 99,7%.

Tableau 5 : Comparaison des densités de mollusques (nombre d'individus par mètre carré) en Meuse entre Namur et Hastière constatées lors des chômages techniques de 1983 et 2012. Source des données de 1983 : Libois & Hallet-Libois, 1987.

	1983	**2012**
Anodonta sp.	4,4	1,6
Unio sp.	1,2	0,2
Dreissena polymorpha	Présence occasionnelle	373,2
Dreissena rostriformis bugensis	/	18,0
Corbicula sp.	/	301,7
Densité totale des mollusques	**5,6**	**694,7**

L'influence des mollusques filtreurs a été modélisée par Pigneur *et al.* (2014). Il a été estimé que les corbicules consommaient, par filtration, 70% de la biomasse de phytoplancton et 75% de la biomasse de zooplancton. De plus, l'augmentation de la respiration des organismes benthiques et la diminution d'organismes planctoniques photosynthétiques pouvait réduire les concentrations d'oxygène dissous, notamment pendant la période estivale avec des pertes maximales estimées par modélisation à plus 2 mgL^{-1}. La productivité de l'écosystème Meuse peut également être modifiée via la redirection des ressources organiques carbonées de la colonne d'eau vers le benthos.

Les modifications anthropiques de la Meuse ne sont pas limitées uniquement à la physico-chimie: au cours du $XX^{ème}$ siècle, de nombreux aménagements hydrauliques ont été menés afin de limiter les risques de crues et de permettre la navigation (Figure 16). Ce n'est toutefois que lors de la seconde moitié de cette période que la partie belge de la Meuse a subi les aménagements les plus importants. Afin de permettre la circulation de péniches de grand tonnage (1350 – 2000 tonnes) depuis le port d'Anvers, le lit mineur de la Meuse a été approfondi et de nombreux barrages automatisés ont vu le jour. En plus d'homogénéiser les habitats du lit mineur, l'approfondissement de la rivière a également diminué le potentiel d'accueil des plantes aquatiques. Les berges ont également été stabilisées à l'aide de techniques d'aménagement telles que des murs bétonnés verticaux, des enrochements, etc.,

réduisant la végétation littorale et la ripisylve et limitant les échanges du lit mineur vers le lit majeur. En France, en revanche, en amont d'Ham-sur-Meuse, la Meuse a conservé des caractéristiques hydromorphologiques diversifiées. La Meuse y est non navigeable et seules les péniches de faible tonnage (300 tonnes) peuvent accéder au canal de l'Est via un canal de dérivation (canal Freycinet).

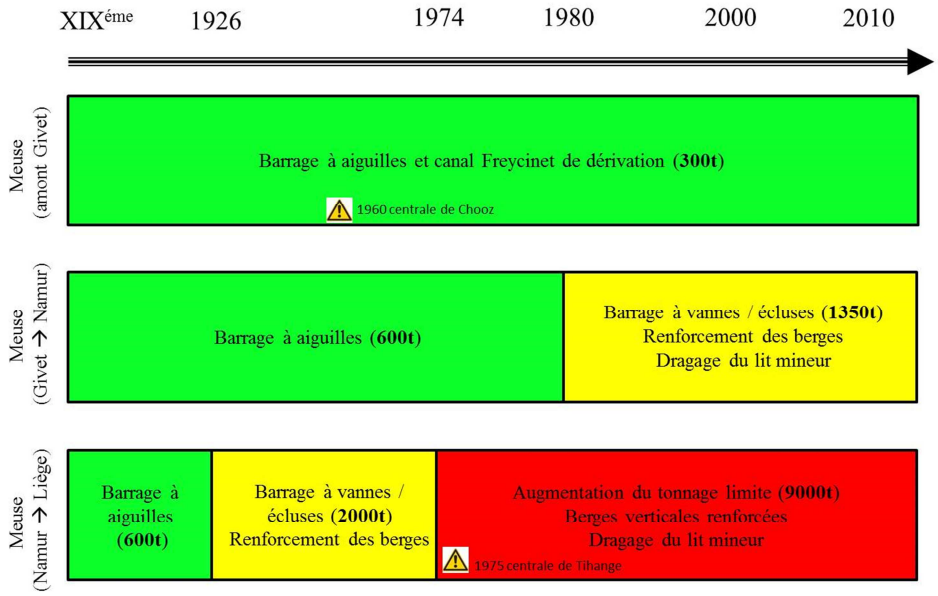


Figure 16 : Evolution des aménagements liés aux transports fluviaux de la Meuse belge et française

L'essentiel du trafic fluvial de marchandise transitte par la Meuse entre Liège et Namur, le linéaire de la Meuse situé en amont de Namur est relativement peu employé et représentait 2,6% du trafic circulant en 1986 (Figure 17).

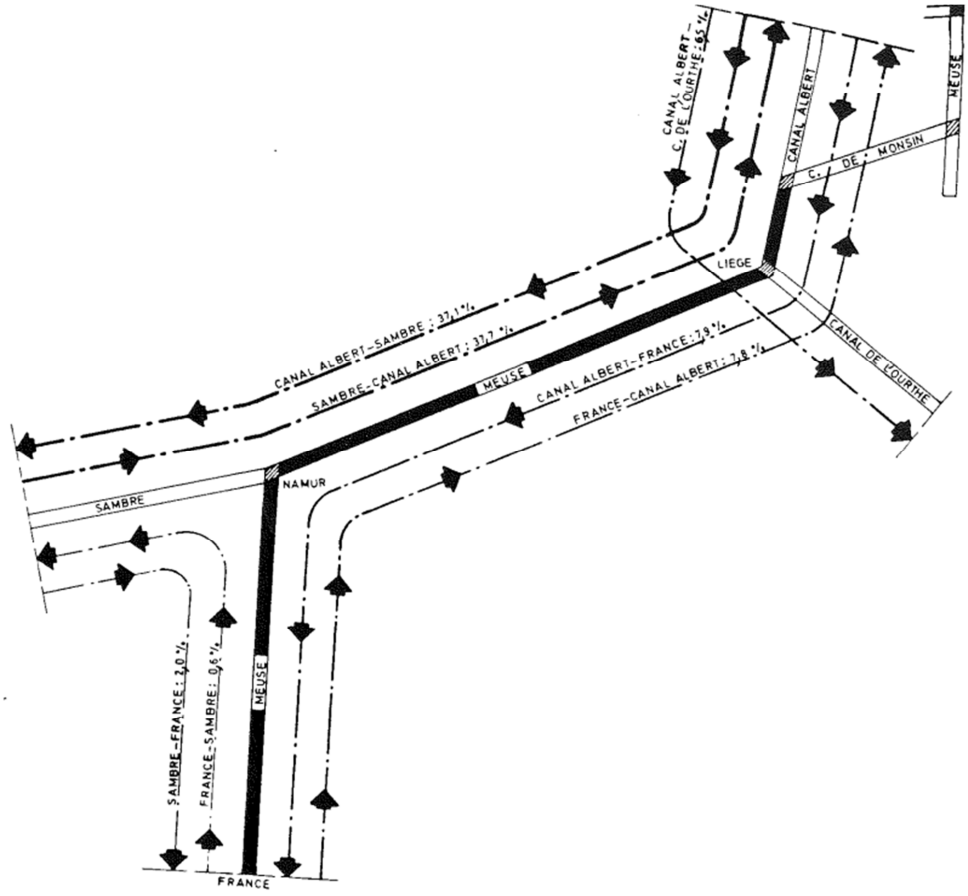


Figure 17 : Ligne du trafic de transit sur la Meuse en 1986 (100% = 139835 tonnes de marchandises). (Micha & Pilette, 1988)

Notre étude (Tableau 6 et Figure 13) considère le linéaire de la Meuse allant de Saint-Mihiel (Pka=172, France) à Liège (Pka=599, Belgique).

Tableau 6 : Brève description morphologique des différents biefs étudiés.

Site	**P.k.a.** (km)	**Superficie du bassin versant** (km2)	**Largeur du lit mineur** (m)	**Débit moyen** (moyenne annuelle $m^3.s^{-1}$)	**Altitude** +/-5 m	**Pente** (/1000)
Han / Meuse	172	2544	35	31	217	0.13
Saint-Mihiel	175	2548	35	31	215	0.12
Sassey/Meuse	283	3683	35	45	171	0.08
Inor	305	3899	40	48	163	0.06
Ham / Meuse	469	10110	100	148	105	0.13
Hastière	489	10584	120	152	95	0.25
Tailfer	522	12560	95	171	82	0.17
Liège	599	20323	140	263	57	0.26

Au cours de cette étude, nous nous pencherons plus précisement sur deux stations, Ham-sur-Meuse et Hastière (Waulsort) qui, bien que distantes de moins de 20 km, sont très distinctes en termes de gestion hydromorphologique.

b. Description de la station d'Ham-sur-Meuse

Le secteur étudié de la station d'Ham-sur-Meuse est localisé en amont de la centrale nucléaire de Chooz entre l'Islon Judas et l'île du Paradis (figure 18). Ce tronçon distant d'approximativement 469 km de la source mesure 1500 m de long et est situé en zone non-navigable. Ce secteur de la Meuse a conservé la plupart de ses fonctionnalités écologiques du fait de sa végétation littorale et riparienne bien développée, de sa connection au lit majeur autorisant la présence d'annexes hydrauliques (bras morts…) et surtout de la faible profondeur de son lit mineur facilitant l'implantation de végétataux aquatiques (Figures 19 et 20).

Figure 18 : Vues générales de la Meuse à Ham-sur-Meuse depuis l'amont (haut) et l'aval (bas) du pont (50°06'53.2"N, 4°47'05.6"E)

Figure 19 : Visualisations de différents habitats présents au niveau de la station d'Ham-sur-Meuse

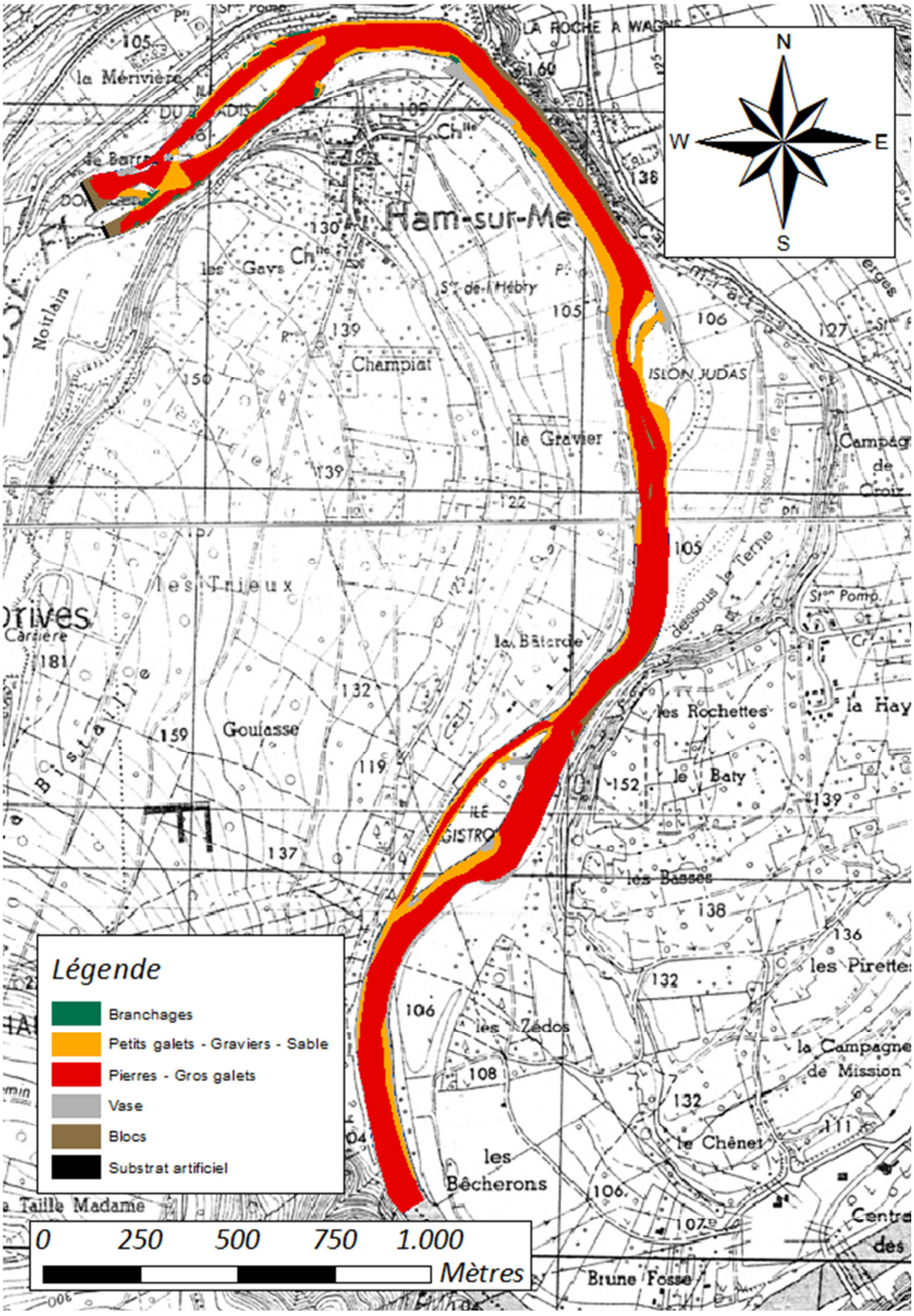


Figure 20 : Cartographie du lit mineur de la Meuse à Ham-sur-Meuse lors du chômage technique d'octobre 2012 (d'après Otjacques et Latli., 2012).

En 2014 la station d'Ham-sur-Meuse a été qualifiée d'un « bon » état écologique (voire « très bon » pour les macrophytes) et d'un « bon » état physico-chimique en dehors des concentrations de certaines molécules chimiques comme le Mercure, qui déclassent l'état chimique du site en « mauvais ». Les pressions humaines restent faibles sur ce secteur de rivière où les milieux forestiers et semi-naturels représentent plus de 87,7% du recouvrement

du bassin versant selon l'Agence de l'Eau Rhin-Meuse. Le débit de la Meuse est légèrement influencé par à un barrage à aiguilles (figure 21).

Figure 21 : Vue du barrage à aiguilles d'Ham sur Meuse (source : *http://www.bameo.fr*)

c. Description de la station d'Hastière-Waulsort

Le secteur étudié de la station d'Hastière-Waulsort est localisé entre le barrage d'Hermeton-sur-Meuse et le pont d'Hastière (figure 22). Ce tronçon distant d'approximativement 489 km de la source mesure 2000 m de long et a été aménagée afin de permettre la navigation de péniches de 1350 tonnes. La ripisylve y est peu développée et le canal principal relativement profond, car dragué, représente la grande majorité du lit mineur (c.f. l'habitat indéterminé de la figure 23). Seuls les bras annexes, proches des îles, ont conservé une profondeur plus faible et un substrat diversifié permettant le développement de la végétation aquatique (figure 24). Selon la Commission Internationale de la Meuse, la qualité physico-chimique est relativement comparable entre la station d'Ham-sur-Meuse et d'Hastière en dehors des concentrations de matières organiques plus importantes en Belgique (Commission internationale de la Meuse, 2011).

Figure 22 : Vues générales de la Meuse à Hastière-Waulsort depuis l'amont (haut) et l'aval (bas) du pont d'Hastière (50°12'56.8"N 4°49'37.0"E)

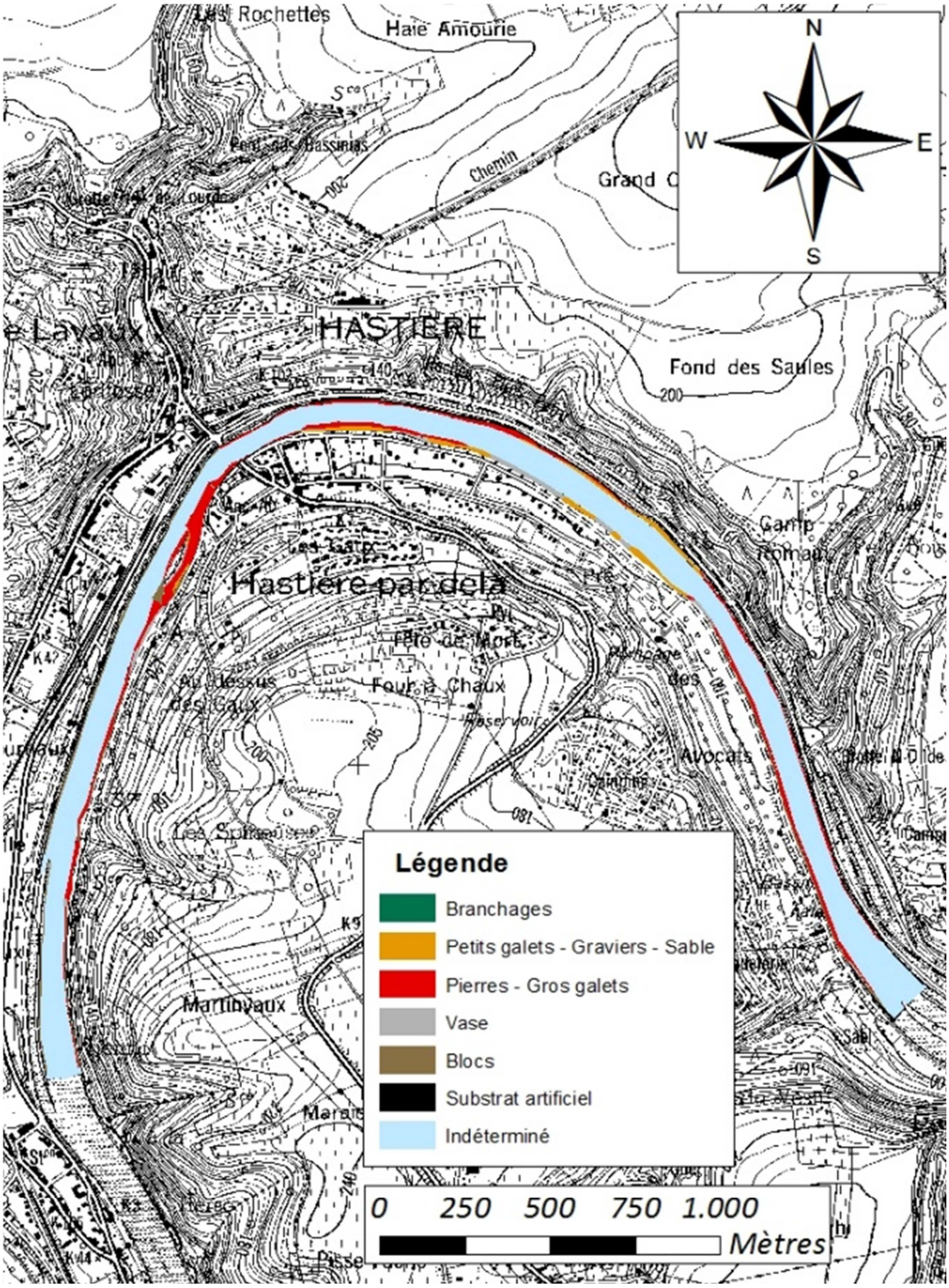


Figure 23 : Cartographie du lit mineur de la Meuse à Hastière-Waulsort lors du chômage technique d'octobre 2012 (d'après Otjacques et Latli., *2012*).

Figure 24 : Visualisations de différents habitats présents sur la station d'Hastière-Waulsort, au niveau de l'île (haut) et du chenal principal (bas).

Le niveau d'eau du bief est controlé par deux barrages automatisés en amont d'Hastière et à Waulsort (figure 25). Ces ouvrages sont équipés de passes à poisson.

Figure 25 : Vue du barrage et de l'entrée de l'écluse d'Hastière (50°12'13.2"N 4°49'09.3"E)

Chapitre 1

Long-term trends in trait structure of riverine communities facing predation risk increase and trophic resource decline

Avant-propos

Dans le chapitre 1er de cette thèse, nous décrivons les grandes tendances environnementales qui ont eu lieu entre 1985 et 2011 sur un long linéaire de la Meuse (427 km) entre Saint-Mihiel (Fr) et Visé (Be). L'idée sous-jacente est de tester l'influence des variations environnementales sur le fonctionnement des communautés de macroinvertébrés et de poissons en réduisant les biais liés à la différence de morphologie/typologie des sites étudiés. L'effet des variables évoluant significativement au cours du temps comme l'abondance du phytoplancton ainsi que le risque de prédation a fait l'objet d'une attention particulière.

Ce chapitre repose sur une collection de bases de données belgo-française adaptée par l'auteur. La base de données « physico-chimique » disponible à l'UNamur-URBE (réalisée par Viroux L. et Descy J.P.) a été mise à jour et homogénéisée. Les bases de données biologiques ont été collectées et mises en forme par le doctorant. L'analyse des données a été exécutée intégralement par l'auteur à l'aide du logiciel R. Les résultats de ce chapitre ont été publiés dans la revue Ecological Applications. Cette publication est le fruit d'une collaboration entre les différents auteurs cités ci-dessous, chapotée par le premier auteur.

Latli A., Descy J. P., Mondy C. P., Floury M., Viroux L., Otjacques W., Marescaux J., Depiereux E., Ovidio M., Usseglio-Polatera P., Kestemont, P., (2017a). Long-term trends in trait structure of riverine communities facing predation risk increase and trophic resource decline. *Ecological Applications*, **27**, 2458–2474

Long-term trends in trait structure of riverine communities facing predation risk increase and trophic resource decline

Abstract

Many large European rivers have undergone multiple pressures that have strongly impaired ecosystem functioning at different spatial and temporal scales. Global warming and other environmental changes have favored the success of invasive species, deeply modifying the structure of aquatic communities in large rivers. Some exogenous species could alter trophic interactions within assemblages by increasing the predation risk for potential prey species (top-down effect) and limiting the dynamics of others via resource availability limitation (bottom-up effect). Furthermore, large transboundary rivers are complex aquatic ecosystems that have often been poorly investigated so that data for assessing long-term ecological trends are missing. In this study, we propose an original approach for investigating long-term combined effects of global warming, trophic resource decrease, predation risk, and water quality variations on the trait-based structure of macroinvertebrate and fish assemblages over 26 yr (1985 – 2011) and 427 km stretch of the river Meuse (France and Belgium). The study of temporal variations in biological, physiological, and ecological traits of macroinvertebrate and fish allowed identifying community trends and distinguishing impacts of environmental perturbations from those induced by biological alterations. We provide evidence, for this large European river, of an increase in water temperature (close to 1 ° C) and a decrease in phytoplankton biomass (-85%), as well as independent effects of these changes on both invertebrate and fish communities. The reduction of trophic resources in the water column by invasive molluscs has dramatically affected the density of omnivorous fish in favor of invertebrate feeders, while scrapers became the major feeding guild among invertebrates. Macroinvertebrate and fish communities have shifted from large-sized organisms with low fecundity to prolific, small-sized organisms, with early maturity, as a response to increased predation pressure.

Introduction

Freshwater ecosystems which are considered as the most vulnerable ecosystems in the world (Malmqvist & Rundle, 2002) have been heavily impacted by human activities, resulting in water pollution, altered water flow and connectivity, habitat loss, fish stock overexploitation and exotic species introduction (Dudgeon *et al.* 2006; Heino *et al.* 2009; Strayer 2010). Large river basins from Western Europe have been especially impaired by these interacting pressures whose individual effects are hardly distinguishable (Floury *et al.*, 2012).

Global warming and biological invasions are considered as synergetic drivers affecting biodiversity (Brook *et al.*, 2008; Walther *et al.*, 2009). Over the last decades, global warming has induced both gradual water temperature increase and hydrological alteration in rivers (Durance & Ormerod, 2009; Walther, 2010; Floury *et al.*, 2013). Moreover, climate change favours the establishment of exogenous species which could present an ecological risk by affecting community structure and ecosystem functions (Strayer *et al.* 2008; Gido *et al.* 2010), particularly in a perturbed ecosystems (Dextrase & Mandrak, 2006).

Emergence of new species may control aquatic community composition and induce a shift in the food web structure, both through predation (top-down control) and/or resource reduction (bottom-up control; Cucherousset & Olden, 2011). While trophic interactions have been well studied, especially in lakes, their role is still debated in the field of community ecology (Matson & Hunter, 1992). Trophic interactions can control community structure through both direct and indirect mechanisms (Batzer, 1998), especially following the introduction of exotic predator species (Geray *et al.*, 2015). Examples of predation impact on aquatic food webs and ecosystem function are those of the cormorant (*Phalacrocorax auritus*), which has been a major factor in the decline of the yellow perch (*Perca flavescens*) in Oneida Lake (Rudstam *et al.*, 2004) or the introduction of the smallmouth bass (*Micropterus dolomieu*) in North American lakes, with several effects on diversity and community structure of littoral and pelagic fish (Zanden & Casselman, 1999). Introduction of predators can induce cascading effects by the consumption of preys which controlled the biomass of primary producers (Schmitz et al., 2010). For example, in an intermittent stream Rodríguez-Lozano and colleagues (2016) found that the presence of Barbus meridionalis, an invertebrate feeder, reduced the rate of leaf degradation by decreasing macroinvertebrate abundance. Another example is that of the Nile perch (*Lates niloticus*) introduction in Lake Victoria, which caused the extinction of numerous species of endemic herbivorous haplochromines (Li & Moyle, 1981) and contributed to the degradation of the lake's ecological status. The strength of these effects differ among species, ecosystems, time scales (Estes *et al.*, 2011) and is often proportional to the degree of disturbance, the complexity and the stability of the ecosystem (Gozlan *et al.*, 2010).

In case of proliferation, engineer species can drastically modify the whole ecosystem structure in a short period of time and could induce resource reductions by entirely restructuring the food web (Vander Zanden & Casselman 1999). Resource limitation increases the trophic competition, alters the abundance and interaction strengths in the community and could force

a diet shift of the resident species particularly for species occupying the same trophic level (Thomsen *et al.*, 2014; David *et al.*, 2017). In the American Great Lakes and rivers, the invasive zebra mussel (*Dreissena polymorpha*) have in only a few years affected native bivalve populations (Lercari & Bergamino 2011), but also most of the other biota, from sediment bacteria (Frischer *et al.* 2000) to piscivorous fish (Daniels *et al.* 2005; Ward & Ricciardi 2007; Higgins *et al*. 2011).

In order to highlight environmental changes, anthropogenic disturbances and trophic interactions, an approach based on trait assemblages at the community scale is more efficient than traditional taxonomic methods (Hughes, 2000)., A trait-based approach can provide an integrative signal of environmental impairment (Mondy & Usseglio-Polatera 2013), and allows reducing variation across ecoregions (Pont *et al*., 2006). Furthermore, prey-predator interactions should be easily highlighted by trait assemblage approaches because predation selection depends more on morphological or behavioural characteristics than on species identity (Green & Côté, 2014).

This study proposes an original approach for statistically testing long-term trends in the trait structure of invertebrate and fish communities in a large, multi-stressed river, with the aim of determining which variables influence communities at the local scale. The River Meuse provides a framework for exploring how community changes occurred over time, because, like many other European rivers, it has been subjected to various anthropogenic pressures : (i) climate change and power plant thermal effluent discharge have contributed to water temperature increase; (ii) river hydraulic management has strongly modified a large part of its course; (iii) substantial water quality changes have occurred over time from both gradual decline in industrial and urban contamination and increased agricultural nutrient inputs, and (iv) alien species have proliferated. In the River Meuse, exotic macroinvertebrates can nowadays represent a major fraction of the benthic community (Usseglio-Polatera & Beisel 2002). Among the most problematic non-indigenous taxa are filter-feeding molluscs such as the zebra mussel, the Asian clam *Corbicula* spp (Marescaux *et al.* 2010) and, more recently, the quagga mussel *Dreissena rostriformis* (Marescaux *et al.* 2012). The current maximum densities of *Corbicula* spp. and invasive mussels in the Meuse River are respectively 900 $ind.m^{-2}$ and 1200 $ind.m^{-2}$ on natural substrates and may exceed 40000 $ind.m^{-2}$ on artificial substrates (Pigneur *et al.* 2014; Marescaux *et al.* 2015). Exotic filter-feeder proliferation has considerably reduced phytoplankton production and plankton biomass in the river (Pigneur *et al.* 2014) and may have been the major cause for the severe decline of native fish (Otjacques *et al.* 2015, 2016). Furthermore, since the beginning of the 1990s, the Great Cormorant (*Phalacrocorax carbo*) has been recorded throughout the year in the Meuse River (Paquet *et al.* 2003). The population increased in France from 4,000 in 1970 to 100,000 birds in January 2007 (Collas and Burgul 2011). The Meuse River has played a role of refuge, especially during severe winters, increasing the pressure of this piscivorous bird on fish communities (Paquet 2011).

This study exploits data from the environmental monitoring of eight sites, covering 26 years and 427 km of the River Meuse course, with a focus on macroinvertebrate and fish communities. Using a set of multivariate and regression partitioning techniques, we examined the relationships between trait-based functional changes, environmental trends and trophic alterations, with the objective of testing three hypotheses:

- Hypothesis 1: Environmental alterations, including the reduction of trophic resource availability partially induced by exotic macroinvertebrates, impacted the invertebrate community more than the fish assemblage;
- Hypothesis 2: The dramatic reduction of planktonic resources induced a shift in the consumer communities, from water column feeders to bottom feeders;
- Hypothesis 3: Predation risk increase has changed the both macroinvertebrate and fish assemblages by promoting fast growing prey species with multiple spawnings per year and early maturity, at the expense of large species with low reproduction rate.

Material and Methods

Study area

The Meuse River rises on the Langres plateau in North-Eastern France (Fig. 1), flows through densely populated areas in Belgium and the Netherlands, and empties into the North Sea, after joining the Lower Rhine. The total length of the river is close to 925 Km for a catchment area of 36,011 km². The main characteristics of the river basin and of the river itself were summarised in Descy *et al.* (see in Tockner *et al.* 2009) and Pigneur *et al.* (2014).

During the last 150 years, the river bed was heavily transformed for navigation and flood control mainly along the Belgian section. Sixteen dams are located along the Belgian sector, six of them being equipped with hydropower facilities. River channelization has profoundly affected depth and current velocity, so that the fish community dominated by rheophilic cyprinids (“barbel zone” according to Huet 1949) turned into a community dominated by limnophilic cyprinids (“bream zone”; Descy *et al.* in Tockner *et al.*, 2009).

By contrast, in France, the navigation has taken place in canals parallel to the main river channel, leaving the river bed unchanged, harbouring more natural and diversified habitats than in the Belgian sector.

The River Meuse supplies two nuclear power plants at Chooz and Tihange. Water quality, decreased along the river course and was significantly degraded downstream of Namur (Fig. 1) by urban and industrial pollution (Descy *et al*. in Tockner *et al.*, 2009) despite of recent improvements related to water treatment and regulation of the use of fertilisers, herbicides and pesticides in the catchment.

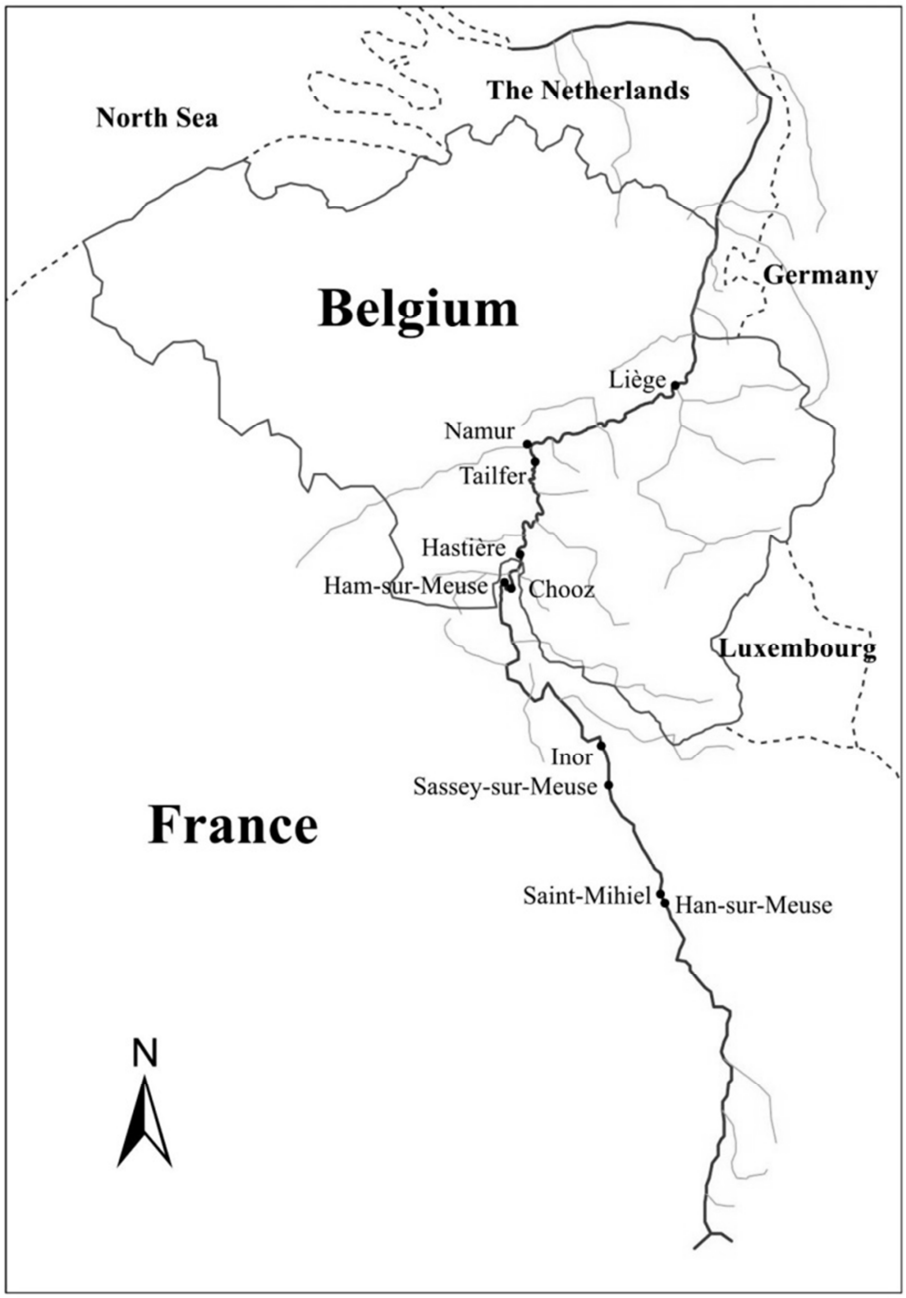


Figure 1: Localization of the River Meuse basin and the sampling sites

Data acquisition

The study was carried out on five homogenous reaches (Tab. 1) located in the French (Han-sur-Meuse, Saint-Mihiel, Sassey-sur-Meuse, Inor, Ham-sur-Meuse) and Belgian (Hastière, Tailfer and Liège) sampling sites of the Meuse River.

Table 1: Physical description of the sampling sites and availability of data (X = data available)

Site	Km from source	Catchment (km2)	Channel Width (m)	Water discharge (annual average $m^3.s^{-1}$)	Altitude +/-5 m	Slope (/1000)	Data availablility			
							Physico-chemical	Macro-invertebrate	Fish	Great cormorant
Han / Meuse	172	2544	35	31	217	0.13			X	
Saint-Mihiel	175	2548	35	31	215	0.12	X			X
Sassey / Meuse	283	3683	35	45	171	0.08		X	X	X
Inor	305	3899	40	48	163	0.06	X			
Ham / Meuse	469	10110	100	148	105	0.13	X		X	
Hastière	489	10584	120	152	95	0.25		X		X
Tailfer	522	12560	95	171	82	0.17	X		X	X
Liège	599	20323	140	263	57	0.26	X	X	X	X

Physical and chemical survey

Physical and chemical data were obtained from public institutions: AERM (Agence de l'Eau Rhin-Meuse) and SPW (Service Public de Wallonie) for France and Belgium respectively. We added data from additional sources, (WACONDAH: "WAter CONtrol DAta system for Hydrology and water management", ISSEP: "Institut Scientifique de SErvice Public", DEMNA: "Département de l'Etude du Milieu Naturel et Agricole", Aquapole). We kept only environmental data series with at least 24 measurements per year to reduce monitoring survey heterogeneity. Five sites, along 424 km of the river course (Saint-Mihiel, Inor, Ham-sur Meuse, Tailfer and Liège; Fig. 1 and Tab. 1), were selected because they had been homogeneously monitored for the longest period of time (1987-2011). Dissolved oxygen ($[O_2]$), water temperature (T), suspended matter ([SM]), nitrate ($[NO_3^-]$), ammonium ($[NH_4^+]$), dissolved reactive phosphorus ($[PO_4^{3-}]$), chlorophyll-a ([Chla]) and water discharge (Q) were measured at these sites by specialized laboratories with reproductive methodologies. For each site and each parameter, annual average values were calculated.

Macroinvertebrate survey

Benthic macroinvertebrates were sampled in summer at Sassey-sur-Meuse, Hastière and Liège from 1998 to 2010 (Tab. 1). At Sassey-sur-Meuse (France) the IBGN ("Indice Biologique Global Normalisé"; NF T90-350, 2004) protocol, or the equivalent (I_2M_2 "MultiMetric Invertebrate Index"; Mondy *et al.* 2012), were used. Eight samples were collected each year with a Surber net sampler (mesh size: 500 µm; sampled area: 0.05 m^2) on diversified habitats. In Hastière and Liège (Belgium), a protocol adapted for deep rivers and derived from the IBGA ("Global Biological Index Adapted to large freshwater rivers", Gay Environnement & Agence de l'Eau Rhône-Méditerranée-Corse 1997) was used (Usseglio-Polatera & Beisel 2002). In these two sites, during each sampling campaign, "stones near the

banks", "aquatic vegetation" and "littoral substrates" were sampled with a hand net (500 µm mesh); the deeper part of the main channel was sampled from a boat using a triangular dredge and three artificial substrates were deployed for one month. Taxon abundances (x) were determined and identification levels were harmonised at the family level. Taxa abundances were log(x+1) transformed to normalize the distributions and rare taxa (i.e. with occurrence ≤ 5% of the sampling events) were not included in the data base to avoid overestimation of rare species or "accidental" captures.

Fish survey

The fish data set gathered information from five sites during 25 years (Tab. 1). In France, electrofishing from a boat along the banks was used in spring, to sample fish assemblages over the 1985-2010 period at Han-sur-Meuse, Sassey-sur-Meuse and Ham-sur-Meuse. In Belgium, data were provided by the survey of fish passages in fish ladders at Tailfer and Lixhe (downstream Liège) over the 1989-2011 period (Matondo & Ovidio 2016). Fish were collected daily in a trap placed in the upper pool of the ladder when the migration peaks occurred, and twice a week outside the major migration period. All the fish species were identified and species abundances were estimated without taking into account the juveniles and the youngs-of-the-year. Annual fish abundances were expressed as monthly averages. Only species exhibiting an occurrence rate of at least 5% over the study period were taken into account. The whole data set was log(x+1) transformed to normalize abundance distributions.

Great Cormorant survey

The Great Cormorant survey was carried out in 5 sites of the studied river sector - Saint Mihiel, Sassey-sur-Meuse, Hastière, Tailfer and Liège – from 1997 to 2011. The ONEMA (Office National de l'Eau et des Milieux Aquatiques) for the French sites and Aves-Natagora for the Belgian sites monitored the winter abundance of the Great Cormorant populations following the methodology developed by Marion (2003b). Birds were counted when arriving at their night roosting sites at the same date every month from November to February. In this study, we focused on data collected in January, when populations were well-established (Collas and Burgun 2010).

Data analysis

Trends in environmental responses

Trends in variation of abiotic parameters were examined over the 1987-2011 period using Generalized Additive Models (GAM; Fewster *et al.* 2000). Each physical or chemical variable was standardised by site. Temporal trends in abiotic parameters were modelled as a smooth nonlinear function of time. Autocorrelation error was reduced by adding a residual autocorrelation structure, optimized by minimizing the AIC criterion over several combinations of autoregressive parameters (Zuur *et al.* 2009).

Preliminary trait-based analyses

Before analysing (i) the temporal trends in life history traits of macroinvertebrates and fish and (ii) the potential influence of environmental parameters on such trends, we performed an exploratory analysis. Congruent life-history traits were selected from published European data bases for fish (adapted from Blanck *et al*., 2007) and macroinvertebrates (Tachet *et al*. 2010). We focused on 9 biological and 10 ecological traits (as defined by Tachet *et al.* 2010) for benthic macroinvertebrates (Appendix 1: Tables S1 & S2) and on 11 life-history traits for fish (Appendix 2). Each trait was resolved in different categories (Appendices 1 & 2). Each taxon was coded according to its affinity to each category of a trait using fuzzy coding (Chevenet *et al.* 1994). The resulting relative affinity scores of the taxa were multiplied by their log(x+1)-transformed abundances at a given date (i.e. within a given invertebrate – or fish - assemblage sample). The weighted affinity scores of the categories of each trait were finally divided by their sum, providing the mean (relative) trait profile of the assemblage at a given date (see e.g. Archaimbault *et al.*, 2010 for further details). To illustrate temporal changes in the trait-based structure of invertebrate and fish communities, Fuzzy Correspondence Analysis (FCA, Chevenet *et al.* 1994) was applied to the array gathering the trait profiles of all the sampled assemblages over the study period.

Defining groups of trait categories with homogeneous responses over the study period.

We first searched to assemble trait categories exhibiting similar responses over time and similar correlation levels with abiotic variables. Between-dates Principal Component Analyses (bPCA, Dolédec & Chessel 1987), which maximise the distance between the "sampling years" along the successive bPCA axes (Dettmers *et al.* 2011), were applied to (i) the "abiotic" and (ii) the "biotic" (i.e. trait profiles of assemblages within sites) data tables centred by site over the study period. Centring the data "by site" allows reducing a potential typological or methodological "between-sites" bias. Then, the "abiotic" and "biotic" bPCAs were combined with a co-inertia analysis (CoI) to explore complex and potentially redundant relationships involving environmental and faunal (trait-based) parameters. The correlation between the two studied tables was evaluated with the RV coefficient, a multivariate analogue of the coefficient of determination (Dolédec & Chessel 1994).

We then defined homogeneous groups of trait categories using a hierarchical cluster analysis, applying the Ward's linkage algorithm(Ward, 1963) to the Euclidean distance matrix calculated using the coordinates of trait categories along the two first factorial axes of the CoI (Dray *et al.* 2003).

Trends and responses in trait category group and taxonomic diversity

Trends in relative frequency of cumulative trait category group utilization over time in both invertebrate and fish assemblages were tested with GAM (see § *Trends in environmental responses*) after standardisation of data by site.

A Hierarchical variation Partitioning (HP) approach was applied to identify the physical and chemical predictors which were best correlated with trait category groups. This method, based on a multiple regression, determines the goodness-of-fit of the models corresponding to all the

possible combinations of the independent variables. Then, the procedure evaluates the independent and joint effects of each explanatory variable on the response parameter using a partitioning algorithm (Chevan & Sutherland 1991). This method avoids (i) the multi-collinearity dilemma of the multiple regression approach, (ii) model specificity and (iii) over-fitting modelling (Mac Nally 2000). Statistical significance was assessed with a randomization approach (Mac Nally 2002).
GAM and HP were also used for examining respectively (i) long-term temporal trends in abundance, taxonomic richness and Shannon-Wiener index (Shannon 1948) and (ii) the influence of physical and chemical parameters on these metrics.

Trait category trends following predation risk increase in a multi-stressed environment
Finally, the effects of "bottom-up" and "top-down" controls on feeding habit and reproductive strategy trends in macroinvertebrate and fish communities were modelled. We related the proportions of scrapers, deposit feeders and predators within the invertebrate assemblage and the proportions of omnivorous and invertebrate feeders within the fish assemblage, to potential shifts in predation pressure and/or trophic resource availability. Similarly, we related to the same potential shifts, the proportions of small-sized (maximal potential size ≤ 0.5 cm) *vs.* large-sized (≥ 4cm), short-lived (life cycle duration < 1 yr^{-1}) *vs.* long-lived (≥ 1 yr^{-1}), thermophilic (T ≥ 15°C) *vs.* psychrophylic (T < 15°C) invertebrates, and the proportions of small/medium-sized (adult body length ≤ 20 cm) *vs.* large-sized (> 20 cm) fish, with low (≤ 1 yr^{-1}) *vs.* high (> 1 yr^{-1}) annual number of spawning events and early (≤ 2 yr) *vs.* late (> 2 yr) maturity. Chlorophyll a concentration was selected as marker of primary trophic resources. The abundances of invertebrate-feeding fish and Great cormorant were selected as indicators of predation pressure for macroinvertebrates and fish, respectively. We included (T) and [PO_4^{3-}] in the models, for taking into account global warming and pollution by domestic waste waters, respectively. In order to simplify the model we did not include environmental variables which did not vary significantly over time (Tab. 2).
Analyses were carried out in the R-software (R 3.1.2 version, R Development Core Team, 2010) using the packages "ade4" (Dray & Dufour 2007) for multivariate analyses, "mgcv" (Wood 2001) for trend analyses and "hier.part" (Walsh *et al.* 2003) for hierarchical partitioning. The statistical methodology is summarized in appendix 3.

Results

Trends in environmental responses
According to the GAM, [Chla] (R^2 = 0.63, P < 0.001), [SM] (R^2 = 0.08, P = 0.049), [NH_4^+] (R^2 = 0.17, P = 0.001) and [PO_4^{3-}] (R^2 = 0.59, P < 0.001) decreased significantly in the Meuse river over the 1987-2011 period, whereas water temperature increased significantly (R^2 = 0.23, P < 0.001) (Tab. 2). Discharge, dissolved oxygen and nitrate did not show any significant temporal trend. The decrease in [Chla] and [PO_4^{3-}] was substantial, with annual mean concentration divided by seven and three respectively, between the late 1980s and 2011. Suspended matter and ammonium concentrations also varied over the same period (Fig. 2).

Table 2: Results of the GAM trend tests applied to physical and chemical parameters measured on five sites of the Meuse River over the 1987-2011 period.

Parameter	Trend	R^2 adjusted	P
Chl *a*	↘	**0.63**	**<0.001**
SM	↘	**0.08**	**0.049**
NH_4^+	↘	**0.17**	**0.001**
NO_3^-	–	0	0.97
PO_4^{3-}	↘	**0.59**	**<0.001**
O_2	–	0.06	0.097
Q	–	0.06	0.18
T	↗	**0.23**	**<0.001**

Note: SM, suspended matter; *Q*, water discharge; *T*, water temperature. Significant values are in bold.

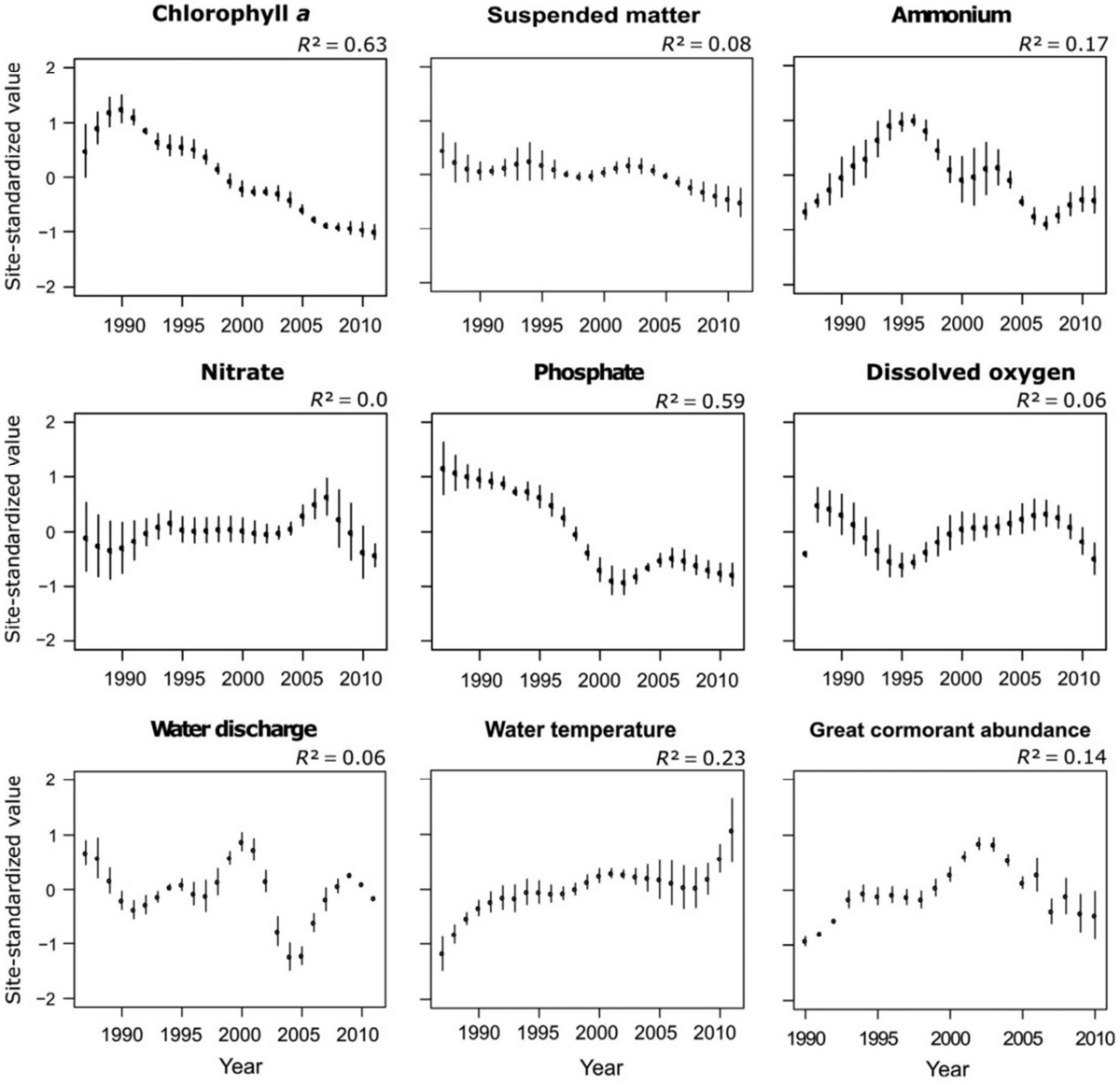


Figure 2: Long-term variation in the annual mean values of the physical and chemical parameters and estimated abundance of the Great cormorant (*Phalacrocorax carbo*) of the

river Meuse between 1987 and 2011 (dark circle) modelled with GAM. Between-sites deviations (= standard deviation bars) are provided. Data have been standardized "by site".

Trends in trait category group responses

The co-inertia analysis examining the common structure of macroinvertebrate traits and physical and chemical parameters over the 1998-2011 period highlighted rather strong relationships between the two sets of data (RV = 0.52; Appendix 4). The $F1_{MI}$-axis, explaining 78% of the variance in trait category utilization, was clearly related to temporal changes, with [Chla] and [SM] strongly and negatively related to the coordinates of trait categories along this factorial axis. The variations in other environmental variables did not importantly explain community trait variation along $F1_{MI}$-axis or were more related to $F2_{MI}$-axis variations (explaining only 10% of the total variance; Appendix 4).

Six groups of trait categories ($T1_{MI}$ to $T6_{MI}$) were defined using their coordinates on the two first factorial axes of the CoI. The relative utilization of trait categories from groups $T1_{MI}$ and $T2_{MI}$ significantly ($p < 0.001$) decreased over the study period ($R^2 = 0.32$ and 0.35, respectively). Such variations were significantly related to [Chla] ($R^2 = 0.15$) and [SM] ($R^2 = 0.14$) variation over the study period (Fig. 3 and Tab. 3). In contrast, the abundance of $T6_{MI}$ increased over time ($R^2 = 0.19$) and could be significantly related to decreasing [Chla] and [NH_4^+] ($R^2 = 0.12$ and 0.093 respectively). The other groups did not exhibit clear temporal trends. Temperature only influenced the abundance of $T3_{MI}$ ($R^2 = 0.12$; Tab. 3).

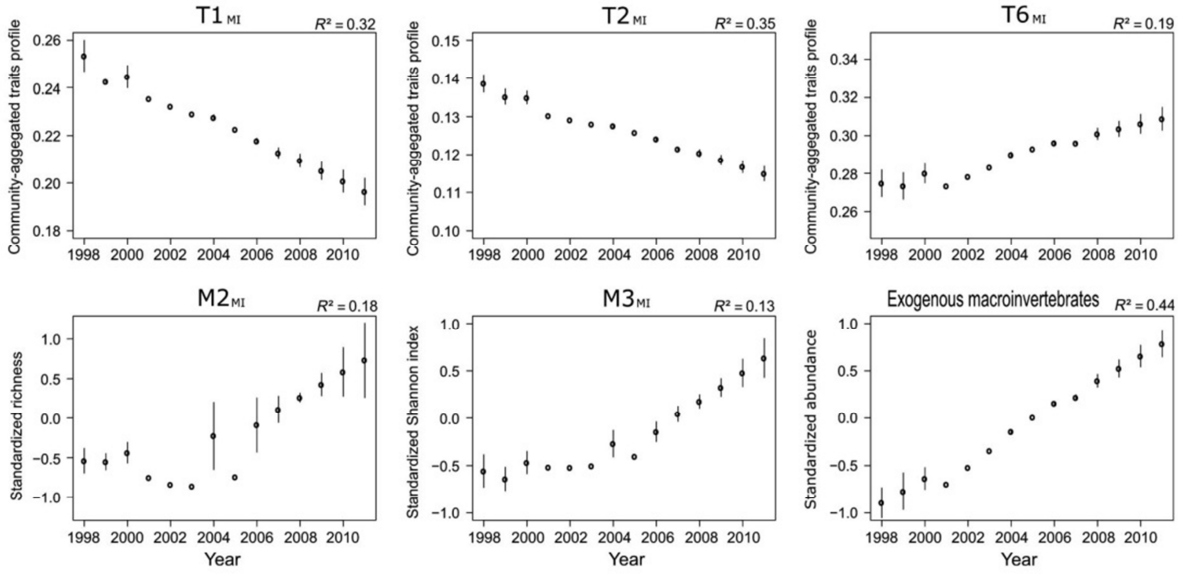


Figure 3: Long-term variation in the relative abundance of three trait category-based groups ($T1_{MI}$, $T2_{MI}$, and $T6_{MI}$), two structural indices [richness ($M2_{MI}$) and Shannon-Wiener index ($M3_{MI}$)] and exogenous taxa describing the invertebrate assemblage in three sites of the River Meuse between 1998 and 2011. General temporal trends were modelled with GAM and represented by dark circles. Between-sites deviations were illustrated by vertical bars. Data were standardized by site. Groups were defined by hierarchical cluster analysis applied to the

matrix of Euclidean distances based on CoI taxon scores in the first factorial plane. See appendices 1 and 4 for group details.

The frequency of the groups T1MI and T2MI, decreased over time (Tab. 3): they include essentially large sized organisms with low life circle duration (Appendix 1: table S1). These groups comprised predators and deposit-feeders as well as taxa exhibiting preferences for conditions usually prevailing in headwaters [e.g. low temperature (<15°C), fast current velocity and low nutrient concentration]. Also included in these groups were several other categories of ecological traits [e.g. low pH sensitivity (6/6), longitudinal distribution (5/8), salinity (1/2) and temperature (2/3) preferences] which were related to the temporal gradient (Appendix 1: table S2). Conversely, in T6MI, we found several categories of traits commonly found in disturbed downstream river sections (small taxa with short life duration preferring warm, eutrophic, brackish waters) (Appendix 1: tables S1 & S2). The other groups (T3-5MI) included several traits categories which did not exhibit clear temporal trends [e.g. dispersal, respiration, locomotion, substrate preferendum…].

Table 3: Results of the GAM trend tests applied to (i) the abundances of six homogeneous combinations of trait categories ($T1_{MI}$ to $T6_{MI}$) or (ii) the values of three taxonomy-based metrics [$M1_{MI}$(abundance), $M2_{MI}$(richness) and $M3_{MI}$(Shannon index)] (iii) the abundance of exogenous taxa (Exotic $_{MI}$) in the Meuse River over the 1998-2011 period. Independent contributions of physico-chemical parameters to variations in the abundances of trait-based groups or in the taxonomic metric value variations over the study period are provided. (* $P <$ 0.05, ** $P < 0.01$, *** $P < 0.001$).

	Temporal trend		Independent contribution (%)							
Trait	Trend	R^2 adj (/1)	Chl *a*	SM	NH_4^+	NO_3^-	O_2	PO_4^{3-}	*Q*	*T*
$T1_{MI}$	↘	**0.32*****	**15.3****	**13.6****	**11.5***	1.5	3.1	3.8	5.4	0.7
$T2_{MI}$	↘	**0.35*****	**15.4*****	**13.7***	8.8	10.2	0.6	1.1	2.1	1.2
$T3_{MI}$	–	0.13	**21.9*****	1.8	0.7	1.3	2.4	0.6	1.8	**12.1****
$T4_{MI}$	–	0.04	2.6	3	0.3	10	1.1	4.4	0.4	0.8
$T5_{MI}$	–	0.04	0.2	0.3	0.2	0.8	3.7	1.5	0.1	10.5
$T6_{MI}$	↗	**0.19***	**11.8***	9.1	**9.3***	0.6	0.3	0.3	0.8	1.9
$M1_{MI}$	–	0.02	1.8	0.7	0.8	0.3	**15.6*****	0.8	**17.4*****	3.6
$M2_{MI}$	↗	**0.18***	4	1.2	**13.3***	0.4	0.6	**10.5***	1.4	0.2
$M3_{MI}$	↗	**0.13***	2.4	2	3.7	0.3	1.4	**17.4*****	1.6	0.1
$Exotic_{MI}$	↗	**0.44*****	**9.9***	7.5	**15.0****	0.3	0.2	4.4	8.0	3.0

Note: Independent contributions of physicochemical parameters to variations in the abundances of trait-based groups or in the taxonomic metric value variations over the study period are provided. Significant values are in bold.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

In each group, trait categories followed the same trend during the study period. The relative utilization of more than 57 % of the trait categories included in $T1_{MI}$, $T2_{MI}$ and $T6_{MI}$ significantly changed versus only 15 % of the trait categories belonging to groups $T3_{MI}$, $T4_{MI}$ and $T5_{MI}$ (Appendix 1: tables S1 & S2).

Total macroinvertebrate abundance did not vary significantly over time (Fig. 3 and Tab. 3), contrary to taxonomic richness and Shannon-Wiener diversity index which increased over time (R^2 = 0.02, 0.18 and 0.13 respectively) and were negatively related to nutrient

concentration variation (Tab. 3). The abundance of exogenous invertebrates increased in relation with [NH_4^+] and [Chla] (R^2 = 15.0 and 9.9 respectively).

Matching fish community trait-based structure with environmental changes by co-inertia analysis provided a RV value equal to 0.42 (Appendix 5). The $F1_{FI}$-axis, taking into account 84% of the total variance in the data, highlighted clear temporal changes. The variance explained by $F2_{fish}$ was far lower (8%). Three groups of trait categories were defined ($T1_{FI}$ to $T3_{FI}$): trait categories from $T1_{FI}$ were less and less used (Fig. 4, Tab. 4, trait category composition in Appendix 2) within the fish assemblage (R^2 = 0.24). Trait categories corresponding to groups $T2_{FI}$ and $T3_{FI}$, did not exhibit any significant temporal trend (R^2 = 0.06). [Chla], [PO_4^{3-}], [NH_4^+] and [NO_3^-] were the most important variables related to temporal changes in fish community traits (Tab. 4, Appendix 5), the other physico-chemical variables being poorly involved in $F1_{FI}$-axis.

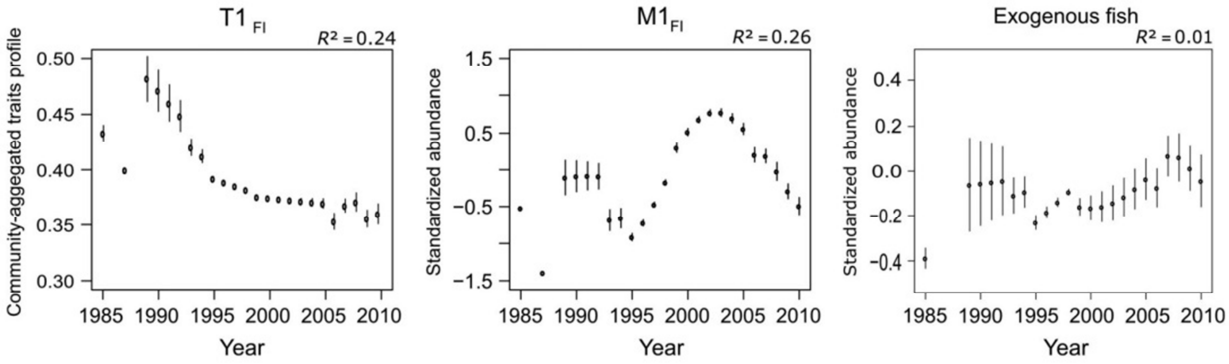


Figure 4: Long-term variation in the relative abundance of one trait category-based group ($T1_{FI}$), one structural index (abundance; $M1_{FI}$) and exogenous taxa describing fish assemblages in five sites of the River Meuse between 1985 and 2010. General temporal trends were modelled with GAM and represented by dark circles. Between-sites deviations were illustrated by vertical bars. Data were standardized by site. Groups were defined by hierarchical cluster analysis applied to the matrix of Euclidean distances based on COI taxon scores in the first factorial plane. See appendices 2 and 5 for group details.

The relative utilization of 66 % of the trait categories included in $T1_{FI}$ significantly changed versus only 4.5 % of the trait categories belonging to $T2_{FI}$ (Appendix 2). Trait categories in relation with feeding habits (omnivorous), body length (> 20-40 cm), number of annual spawning events (< 1) and maturity (at 3 yr), were included in $T1_{FI}$ which was significantly correlated to [Chla] and [PO_4^{3-}]. Although $T3_{FI}$ did not exhibit clear temporal trends, 43 % of the trait categories increased over time (Appendix 2) [e.g. abundance of invertebrates feeders and small sized taxa (<10 cm) with multiple spawnings per years].

Fish abundance increased (R^2 = 0.26; Fig. 4), but species richness, taxonomic diversity and abundance of exotic fish species did not show any significant temporal trend over the study period (Tab. 4).

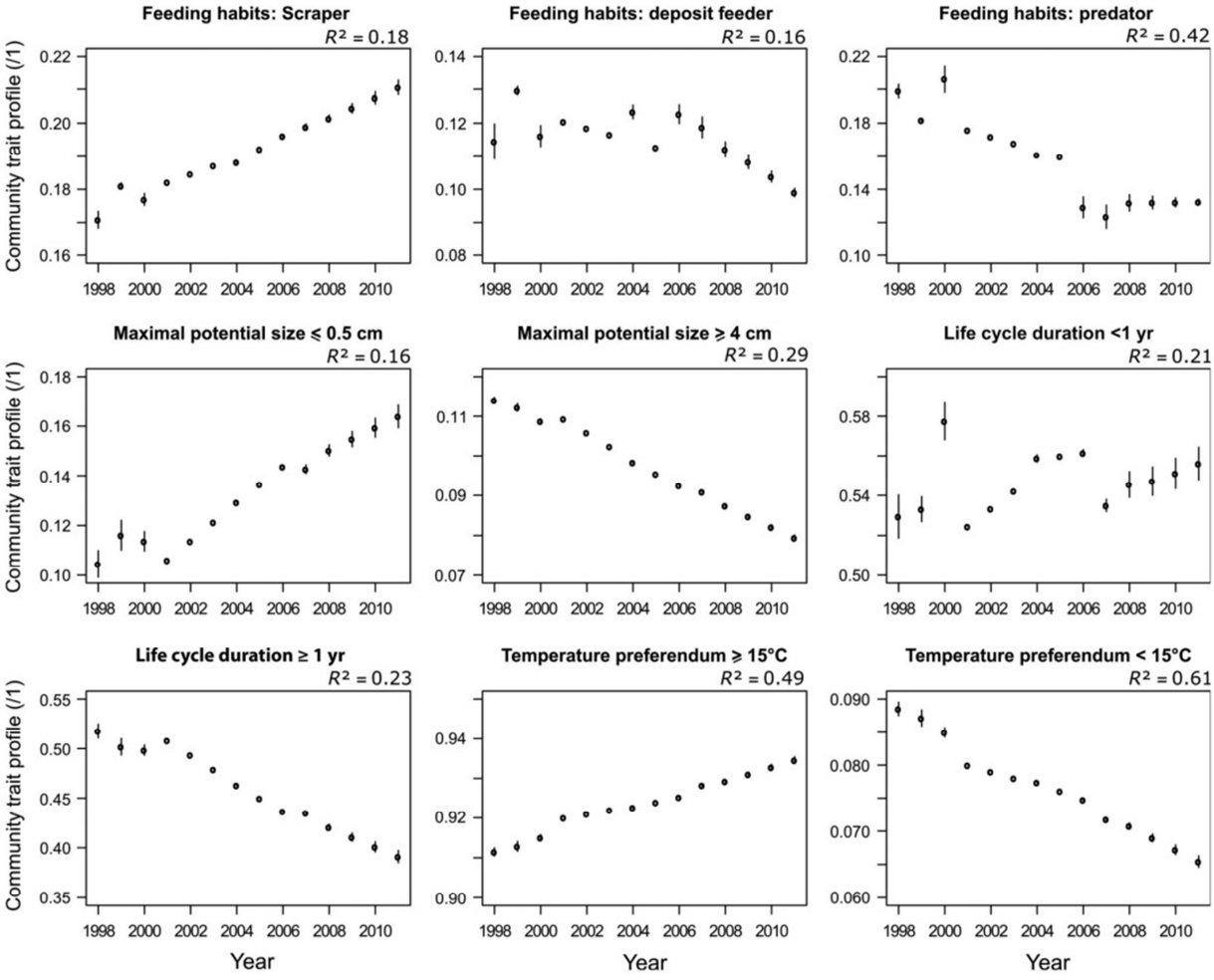
Table 4: Results of the GAM trend tests applied to (i) the abundances of three homogeneous combinations of fish trait categories (T1FI to T3FI) (ii) the values of three taxonomy-based metrics [M1FI(abundance), M2FI(richness) and M3FI(Shannon index)] (iii) the abundance of exogenous taxa (Exotic FI) in the Meuse River over the 1985-2010 period. Independent contributions of physical and chemical parameters to variations in the abundances of trait-based groups or in taxonomic metric value variations over the study period are provided. (*P < 0.05, ** P < 0.01, *** P < 0.001).

	Temporal trend		Independent contribution (%)							
Traits	Trend	R^2 adj (/1)	Chl *a*	SM	NH_4^+	NO_3^-	O_2	PO_4^{3-}	*Q*	*T*
$T1_{FI}$	↘	**0.24****	**7.5*****	0.3	1.6	0.3	6.3**	**16.5*****	0.2	0.3
$T2_{FI}$	–	0	1.7	0.2	**4.4***	**10.6*****	0.4	0.2	0.1	0.6
$T3_{FI}$	–	0.01	2.3	0.1	0.2	2.2	2.8	**9.5*****	0.2	0.2
$M1_{FI}$	↘	**0.26****	1.8	0.4	0.5	1.4	0.5	**6.6****	0.6	0.3
$M2_{FI}$	–	0	0.2	0.4	1.8	3	0.1	0.3	4.2	0.1
$M3_{FI}$	–	0	0.5	0.4	1.1	0.1	0.3	0.2	**6.7****	0.1
$Exotic_{FI}$	–	0.01	0.5	**5.0***	0.4	4.2	0.6	1.0	0.2	0.3

Trait category trends following predation risk increase in a multi-stressed environment

The abundance of predators (R^2 = 0.42) and deposit feeders (R^2 = 0.16) decreased over time with the decline in [Chla], in contrast with the increasing abundance of scrapers (R^2 = 0.18) (Tab. 5, Fig. 5). The abundance of filter-feeders, piercers and shredders remained rather constant (Appendix 1: Table S2).

Figure 5: Spatio-temporal variations in the mean utilization frequency of nine trait categories by the macroinvertebrate assemblage of the Meuse River during the 1998-2011 period. General trends were modelled with GAM and represented by dark circles. Between-sites deviations are illustrated by vertical bars. Associated R^2 coefficients are provided.



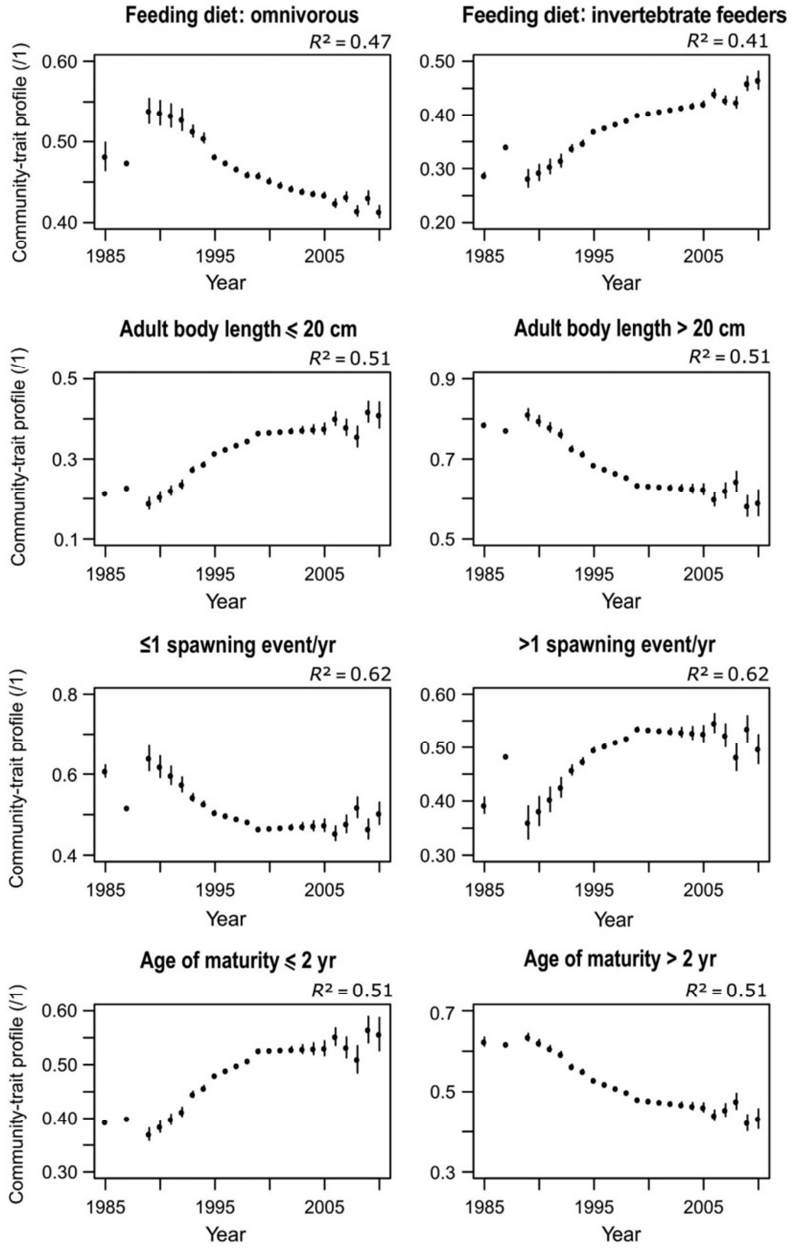
The proportion of small-sized invertebrates (potential length ≤ 0.5cm), and/or with short life span (< 1 yr) increased in the macrobenthic community during the study period (R^2 = 0.16 and 0.21, respectively) at the expense of larger species (potential length ≥ 4 cm) and/or with longer life cycle (R^2 = 0.29 and 0.23, respectively). This trend seemed primarily linked to the abundance of invertebrate feeders and secondly to [Chla] decline (Tab. 5). The proportion of psychrophilic taxa (preferendum < 15°C) decreased over time (R^2 = 0.61) and was statistically related to the decrease in [Chla] (p < 0.001). Thermophilic (preferendum ≥ 15°C° or eurythermic invertebrates increased with increasing water temperature (p = 0.008; Tab. 5, Fig. 5).

Table 5: Results of the GAM trend tests applied to the mean frequency of 17 trait categories in relation with feeding diet or biological strategies exhibited by the macroinvertebrate and fish assemblages of the Meuse River during the study period. Independent contributions of food resources, temperature (T), [PO43-] and predation on each trait category utilization are provided. (*P < 0.05, ** P < 0.01, *** P < 0.001).

	Temporal trend		Independent contribution (%)				
Parameter	Trend	R^2 adj (/1)	Chl *a*	PO_4^{3-}	*T*	Abundance of invertebrate feeders	Abundance of Great Cormorant
Macroinvertebrate							
Feeding habits							
Scrapers	↗	**0.18**	**10.3***	0.2	2.0	**14.6****	–
Deposit feeders	↘	**0.16**	0.7	**117***	1.1	**7.4***	–
Predators	↘	**0.42**	**39.9*****	4.0	0.2	2.8	–
Maximal potential size							
≤0.5 cm	↗	**0.16**	1.2	4.7	0.7	**21.5*****	–
≥4 cm	↘	**0.29**	**12.0***	0.8	1.4	**12.7***	–
Life cycle duration							
<1/yr	↗	**0.21**	0.4	1.5	0.0	0.1	–
≥1/yr	↘	**0.23**	**11.8***	4.2	2.7	1.2	–
Temperature preference							
<15°C	↘	**0.61**	**37.3*****	1.2	0.2	2.6	–
≥15°C and eurythermic	↗	**0.49**	0.7	0.7	**15.5****	1.2	–
Fish							
Feeding diet							
Omnivorous	↘	**0.47**	**9.8*****	**17.6*****	0.3	–	6.3
Invertebrate feeders	↗	**0.41**	**10.2*****	**20.0*****	0.3	–	2.8
Adult body length							
≤20 cm	↗	**0.51**	6.6	**16.8*****	0.5	–	**19.2*****
>20 cm	↘	**0.51**	6.6	**16.8*****	0.5	–	**19.2*****
Number of spawning events							
≤1/yr	↘	**0.62**	4.6	**9.3****	0.4	–	**16.2*****
>1/yr	↗	**0.62**	4.6	**9.3****	0.4	–	**16.2*****
Age of maturity							
≤2 yr	↗	**0.51**	3.8	**8.5****	0.5	–	**24.5*****
>2 yr	↘	**0.51**	3.8	**8.5****	0.5	–	**24.5*****

The potential diet and life-strategy of fish changed substantially during the study period. In parallel with the decline in [Chla] and [PO_4^{3-}] (Tab. 5, Fig. 6), the abundance of invertebrate feeders increased (R^2 = 0.41) while the abundance of omnivorous species decreased (R^2 = 0.47). Small-sized fish (≤ 20 cm), with early maturity (≤ 2 yr) and multiple spawning over the year increased over time (R^2 = 0.51, 0.51 and 0.62, respectively), primarily in relation with the increasing abundance of the Great Cormorant ($p < 0.001$) and secondly with the decrease in [PO_4^{3-}] (Tab. 5).

Figure 6: Spatio-temporal variations of the mean utilization frequency of eight trait categories by the fish assemblage of the Meuse River during the 1985-2010 period. See Figure 5 for further details.



Discussion

In this study, we have demonstrated that environmental changes and predation risk increase spanning three decades may have impacted the trait-based structure of the benthic macroinvertebrate and fish assemblages in a large river.

Causes of environmental changes and consequences on the trait-based structure of invertebrates and fish community.

Our data provide evidence for a significant increase in mean annual water temperature in the River Meuse, as a result of climate change and other anthropogenic impacts, with an average

increase of about 1°C over 24 years. A similar trend has been observed in other West-European large rivers, including the Rhône (Fruget *et al.*, 2001), the Danube (Webb & Nobilis, 2007), the Loire (Floury *et al.* 2012), the Rhine (Van Vliet *et al.*, 2013) and several rivers in southern England (Durance & Ormerod, 2007). In the latter, water temperature increased between 1.2 and 1.7°C from 1981 to 2005, especially in winter (+2.1-2.9°C). By contrast, no trend was detected for dissolved oxygen concentration and water discharge in the Meuse River over the 1987-2011 period. However, the calculation of annual averages obviously precludes examining possible variations at shorter time scales. For instance, under climate change, the hydrological regime of the Rhine River exhibited higher winter and lower summer flows *(*Middelkoop *et al.* 2001). In the River Meuse, multi-year cyclic variations have been observed during the 30 last years , with low flow periods alternating with high flow periods (Descy et al., in Tockner *et al.*, 2009).

An important change that has occurred in the River Meuse over the last 24 years is the major decrease in chlorophyll-a concentration. The reduction of 85% of the phytoplankton biomass is correlated with the rise of exotic macroinvertebrates (Tab. 3) which became more abundant (Fig. 3). For examples, Pigneur *et al.* (2014) provided evidence that the invasive Asian clams *Corbicula* spp**.** have played a major role in the decline of chlorophyll a. In parallel with this apparent diminution of eutrophication, the water quality of the Meuse River has actually improved, due to waste water treatment in France and Belgium, which reduced nutrient concentration, suggesting that phytoplankton growth may have become P-limited. However, despite orthophosphate concentration decrease, it is still above growth-limiting levels for most phytoplankters (Pigneur *et al*., 2014). Accordingly, we found poor correlation between chlorophyll-a and nutrient concentrations. Actually, the decline in phytoplankton biomass has reduced the phosphorus demand, making phosphorus limitation even less likely. The situation is somewhat different in other large rivers, e.g. the Loire River, where integrated water management for eutrophication control has resulted in effective nutrient limitation of phytoplankton growth (Descy *et al.*, 2012) and substantial changes in biogeochemical cycles (Minaudo *et al.* 2015). To some extent, the successful colonization of the Meuse River by exotic filter-feeders has mitigated the effects of eutrophication: despite rather high nutrient concentrations and improved underwater light climate due to long-term decrease in suspended matter (Descy *et al*. in Tockner *et al.*, 2009), the phytoplankton biomass decreased, allowing an improvement of the water quality and transparency. However, our study shows that the strong reduction of the autochthonous contribution to the particulate organic carbon flux has strongly influenced the consumers' community structure in the Meuse River.

Our study points out the major role of chlorophyll-a concentration, and by contrast a much lower effect of water temperature on long-term trends in the trait-based structure of the macroinvertebrate and fish assemblages in the Meuse River (Tab. 3 & 4), with a stronger impact on macroinvertebrates than on fish. Indeed, many more (41% of the total categories considered) macroinvertebrate traits changed over time than in fish (Appendices 1 & 2). Furthermore, macroinvertebrate trait-groups showed a stronger relationship with water quality variables. These results agree with Marzin *et al*. (2012), who found that macroinvertebrates

were more sensitive to environmental degradation at low pressure level than fish, which exhibited a stronger response to high pressure level, due to their longer life cycle and their migratory behaviour. In a lowland stream, sensitive macroinvertebrate taxa responded mostly to organic pollution and hydromorphological stress whereas fish reacted more strongly to flow disturbance (Poff & Zimmerman, 2010). Similar results, i.e. that primary consumers responded better to changes in nutrient and temperature patterns, were found by others (Gafner & Robinson, 2007).

In our study, taxonomic-based metrics of both macroinvertebrate and fish communities were mainly correlated to the decrease of nutrient loading (Tab.3 & 4), and independent from changes in chlorophyll-a concentration and water temperature (Tab. 3). This agrees with the results of Durance & Ormerod (2007), Daufresne *et al.* (2007) or Floury *et al.* (2013),. However, we tested the response to annual average temperature, and not to maximal summer temperature, which can affect macroinvertebrate or fish assemblages(Heino *et al.*, 2009). Several studies on riverine fish communities (Chu *et al.* 2005; Daufresne & Boët 2007, Buisson & Grenouillet, 2009) have reported or predicted significant variation in species richness, total abundance and/or taxonomic evenness due to global warming. Identifying more precisely the potential role of temperature on community structure would require additional studies focusing on the effect of altered winter minima and summer maxima.

Effects of resource availability decrease and predation risk increase on the trait-based structure of assemblages in a multi-stressed environment

Our analysis of the Meuse River data also provides evidence of a significant impact of invasive exotic species on the food web, through change in resource availability, competition and predation.

As a result of the arrival and spread of exotic filter-feeders (e.g. *Corbicula spp.*, *Dreissena spp.*…), which dramatically reduced phytoplankton biomass (Pigneur *et al*., 2014), we observed a shift in feeding guilds within the microbenthic assemblage. The river water transparency improvement, due to chlorophyll-a and suspended matter decline (Fig. 4 and Tab. 5), may have benefited to benthic scrapers. This trend is more significant in the upper section of the Meuse River, where the shallower channel promoted periphyton and macrophyte growth. In parallel, a significant decrease in deposit feeders occurred (Tab. 5), as a result of reduced phytoplankton biomass. In large lowland rivers where phytoplankton is abundant, the feeding activity of filter-feeders can redirect the flux of organic matter from the water column to the benthos, thereby enriching sediment and favoring deposit-feeders (Strayer *et al.* 1999; Idrisi *et al.* 2001). Conversely, a reduction of phytoplankton density in the water column can directly affect particulate organic matter supply to the bottom, and thereby impact deposit-feeders. In the River Meuse, the decline of native deposit-feeders can be attributed to fish predation (Tab. 5) but also to competition with exotic crustaceans occupying the same ecological niche. During the 1990s, *Chelicorophium* sp., a Ponto-caspian invasive crustacean, gradually became dominant (bij de Vaate *et al*., 2002, Josens *et al.*, 2005). More recently, the exotic amphipod *Dikerogammarus villosus*, first recorded in the

River Meuse in the early 2000s (Van den Bossche, 2002), has become the most abundant benthic predator and may have contributed to the spectacular demise of the native gammarid species.

In parallel with the chlorophyll-a decline in the River Meuse, the feeding habits of fish assemblage also shifted gradually from a community dominated by omnivorous species to invertebrate-feeding species (Fig. 6 and Tab. 5). Omnivorous fish have been affected by the drastic decrease in zooplankton density (Pigneur *et al.*, 2014) which represented in 2010-2012 less than 2% of the biomass present during the 1990's (unpublished personal data), following the phytoplankton decline. Otjacques *et al.* (2016) confirmed that the main cause for the dramatic reduction of the roach (*Rutilus rutilus*) in the Belgian part of the Meuse River has been the drastic decline in planktonic resources that followed the invasion of the exotic filter-feeders.

Top-down control has also had an important impact on both macroinvertebrate and fish assemblages in the River Meuse. The increase of invertebrate-feeding fish was significantly correlated to the diminution of large species of macroinvertebrates, to the benefit of small-sized species (Tab. 5). However, the trait-based structure of the fish assemblage appears more impaired by predation than that of the benthic macroinvertebrate assemblage. In particular, slower-growing fish species with late maturity and low fecundity (e.g. *Thymallus thymallus, Leuciscus leuciscus, Esox lucius*…) which have significantly declined over the study period, most probably as a result of cormorant predation, whereas changes in macroinvertebrate reproductive strategies are not significantly correlated to fish predation (Tab. 5). While the predation pressure of the cormorant on the fish assemblage is clear and has already been described (Engström, 2001; Cech & Vejrík, 2011), the link between fish predation and macroinvertebrate assemblage abundance seems more complex than initially expected. Several studies have reported highly variable top-down effects due to invertebrate-feeders, depending on the study context (Wallace & Webster, 1996) or the habitat complexity (Diehl, 1992; Everett & Ruiz, 1993).

Conclusions

The results of this study are in accordance with previous research on trait category selection (Statzner *et al.* 2004; Chu *et al.* 2005; Van Riel *et al.* 2006; Buisson & Grenouillet 2009) and have supported our hypotheses, namely, that the functional structure of benthic macroinvertebrate assemblages has been more impacted than that of fish assemblages by the decline of planktonic resources (hypothesis 1), and that the trait-based structure of both communities was significantly correlated (i) indirectly by trophic limitation caused by exotic species invasions (hypothesis 2) and (ii) directly due to predation risk increase (hypothesis 3). However, some interpretations should be carefully considered. When studying long-term effects of physico-chemical variables on communities, ecologists have often to cope with long-term data obtained using various, heterogeneous field and laboratory methodologies. Limiting the potential bias due to sampling heterogeneity over the study period is often a

major challenge, which was met in our case (i) by selecting sites and periods surveyed with the most similar sampling methodologies, (ii) by log-transforming taxon abundances, (iii) by centring the data “by site” to reveal temporal trends and (iv) by using only the family identification level for benthic macroinvertebrates and (v) by using a functional method rather than taxonomic approach (Hering *et al.*, 2006). Even if several authors have pointed out the potential risk of misinterpreting or underestimating the impacts of abiotic pressures on biotic communities when using a rather low taxonomic resolution (Thompson & Townsend, 2000; Bonada *et al.*, 2007) the family-level appeared as a favorable compromise to illustrate evolution of the trait diversity of fish and macroinvertebrate assemblages (Demars *et al.*, 2012). The long-term database, gathered from two independent national survey programs applied with unvaried methodology, has provided consistent results and has demonstrated the high interest of this approach in future management challenges, even at family level for invertebrates.

Finally, our research takes place within a multi-stressor context where it is complex and difficult to statistically explain the variation of a single dependent metric by a specific independent variable because of potential confounding effects. Indeed, in multi-stressed ecosystems, each abiotic or biotic factor can potentially interact with other factors or processes (Daufresne & Boët 2007). This study has highlighted the importance of trophic relationships in community dynamics, the dominant role of new exotic predators in the trophic functioning of rivers and the potential influence of environmental degradation that can unbalance ecosystem functioning by facilitating the establishment of new species or reducing community diversity (Travis, 2003).

Ce qu'il faut retenir de ce chapitre

Dans ce premier chapitre nous décrivons les grandes tendances environnementales et leurs impacts sur le fonctionnement des communautés de macroinvertébrés benthiques et de poissons sur un long linéaire de la Meuse. Afin de ne faire ressortir que les évolutions communes entre les différentes stations, nous réduisons le biais lié à la typologie et à la méthodologie d'inventaire des organismes via différentes approches statistiques (centrage-réduction des données par site, modèle mixte…). Trois grandes tendances se sont dégagées du jeu de données collecté :

- Nous avons démontré que le long du linéaire étudié la biomasse du phytoplancton a significativement diminué au cours des 24 dernières années. Cette réduction a contribué à l'augmentation de la transparence de l'eau favorisant potentiellement le développement du périphyton et de ses consommateurs directs (scrapers). A l'inverse la réduction du seston (phyto-zooplancton) a concouru à l'effondrement des stocks de certains poissons omnivores évoluant principalement dans la colonne d'eau (gardon, ablette commune, vandoise…).
- La pression de prédation sur les communautés de macroinvertébrés et de poissons s'est accrue au cours de la période étudiée du fait de l'augmentation des densités de poissons invertivores et du grand cormoran. La prédation impacte négativement essentiellement les taxons de plus grande taille, à durée de vie élevée et à maturité sexuelle tardive.
- Enfin, la température annuelle de la Meuse a augmenté d'environ 1°C sur la période étudiée favorisant les taxons eurythermes. Cette élévation de la température annuelle peut sembler négligeable, toutefois son influence sur les communautés peut être plus sérieuse durant la période estivale.

Dans ce premier chapitre, nous avons démontré qu'à l'instar de nombreuses rivières Européennes et nord Américaines soumises à de multiples pressions (eutrophisation, invasion biologique, homogénéisation de l'habitat…) les communautées biologiques de la Meuse tendent à se banaliser au profit d'espèces pionnières de petite taille ayant développé des adaptations aux environnements perturbés (Chu *et al.*, 2005; van Riel *et al.*, 2006; Buisson *et al.*, 2008; Buisson & Grenouillet, 2009). Les traits d'histoires de vie décrits précédemment, apparaissent au sein des différentes communautés indépendament des dissemblances hydromorphologiques entre les stations étudiées.

Une analyse taxonomique des assemblages de macroinvertébrés et de poissons décrits lors de cette étude a également été réalisée à l'aide d'une méthodologie similaire. Les résultats des analyses sont disponibles en annexes 8, 9, 10 et 11.

Dans les chapitres suivants nous mettrons en avant l'influence de la gestion hydraulique de la Meuse belge ou française sur les communautés/populations de macroinvertébrés et de poissons via des études comparatives à l'échelle de la station.

Chapitre 2

Structural changes in fish populations and communities in the River Meuse (Belgium) over the last 20 years

Avant-propos

La première partie du 2ème chapitre décrit l'évolution des stocks de gardon (*Rutilus rutilus*), une espèce omnivore largement représentée, sur trois de secteurs de la Meuse belge pendant une période de 20 ans. Au cours de ces deux décennies, les concentrations en plancton ont drastiquement diminué et l'abondance du grand cormoran (*Phalacrocorax carbo*) a augmenté. Cette étude permet également de comparer a posteriori l'évolution de la population de gardons de la Meuse belge aux populations de gardons évoluant en zone non navigeable de la Meuse française (Alonso *et al.*, 2014).

La seconde partie de ce chapitre étudie plus spécifiquement l'évolution des assemblages ichtyologiques de deux sites de la Meuse Belge, Tailfer et Lixhe. Nous avons également testé la corrélation entre différentes pertubations potentielles (la concentration de phytoplancton et la densité de grand cormoran) et l'évolution (taxonomique et fonctionnelle) des assemblages piscicoles à l'aide d'analyses multivariées.

Le doctorant a réalisé la seconde partie de ce chapitre et a participé aux échantillonnages de gardons ainsi qu'à l'analyse partielle des résultats de la première partie. L'analyse des résultats de la dynamique de population à été effectuée par Otjacques W. La première partie de ce chapitre et certains résultats de la seconde partie ont fait l'objet d'une publication dans la revue Fundamental and applied limnology.

Otjacques W, Latli A, Bernard B, Ovidio M, Depiereux E, Kestemont P (2015) Recent decline of roach Rutilus rutilus stock in a large river ecosystem in relation with its population dynamics. *Fundamental and applied limnology*, **187**, 13.

Structural changes in fish populations and communities in the River Meuse (Belgium) over the last 20 years

Abstract

Fish populations in the River Meuse have undergone large structural changes during the two last decades. Roach (*Rutilus rutilus* L.) populations have been investigated by mark-recapture and growth rate and mortality have been assessed by scale reading. It appears that roach stocks have undergone a severe decline. Historical data reveal a stable population in the reach of Tailfer between 1993 and 2003 according to estimates by marking-recapture using the Jackson's positive method. But present data reveal a drastic decrease of 90% in this reach. Investigations have been continued in two other reaches (present study) and results obtained are in the same way. Current roach stocks are very low in the River Meuse. In the reach of Hastière, roach stock has been estimated at 127 roach ha^{-1} and in the reach of Visé, roach density is estimated at 233 roach ha^{-1}. Analysis of CPUEs obtained by gillnetting reflects also the same trend. Current growth parameters present no radical change. Current estimates of exploitation of roach stock are high in the reach of Hastière and similar to past estimates for the reach of Visé. Analysis of fish pass data reveals a deep change in population structure. A significant decrease of passage into fish pass is highlighted. Analysis of trophic guild reveals a change with fish feeding in the water column reflecting roach abundance to more benthivorous fish. A redundancy analysis reveals that decline in plankton biomass is the most correlated variable to explain change in fish population in the reach of Tailfer. In the reach of Visé, Great cormorant (*Phalacrocorax carbo sinensis* Blum.) is the most correlated variable to the decline.

Introduction

Estimates of fish stocks dynamics are employed to evaluate ecological interactions in aquatic communities. These estimates are also important in management to control exploitation of a stock to avoid its collapse in the near future (Peltonen *et al.*, 1999). To highlight abundance and structure of fish population is a real challenge mainly in large river. All sampling methods are biased to some degree when estimates of abundance, richness or distribution are needed (Olin *et al.*, 2009). Estimates of abundance rely on active capture of fish such as gillnetting or electrofishing (Murphy & Willis, 1996). But these methods have their own limits. It is widely known that gillnetting is size selective (Hamley, 1975), tends to underestimate young individuals of a given species or species being more sedentary (Rulifson, 1991). Size selectivity can be reduce by using gillnets with different mesh size (Goffaux *et al.*, 2005). Electrofishing is widely considered as efficient for describing structure populations but is not appropriate for large rivers (Pusey *et al.*, 1998). Moreover electrofishing efficiency is influenced by physical and chemical parameters, swimming capacities of fish (Casselman *et al.*, 1990) and response to electric field may vary between species and size class (Pusey *et al.*, 1998). In large rivers, combination of these two technics allows at the same time sampling of the main channel as of the banks (Goffaux *et al.*, 2005). More, monitoring of fish pass enables data collection on population dynamics and migratory characteristics needed for management of fish populations. The most used technic of counting fish passes is to catch them in a trap disposed within or at the outflows of the pass (Larinier, 1998). Monitoring of fish pass can reveal changes in fish population in a river such as a decline of a particular species (Mallen-Cooper & Brand, 2007).

To assess abundance from capture data, two models are generally employed by biologists (Gatz & Loar, 1988). First, the removal model needs catch data from depletion sampling to give an estimation of density and sampling efficiency. The assumptions are a closed population and the same capture probability for species and sampling (Rosenberger & Dunham, 2005). Second, the mark-recapture model first developed by Petersen (1896) is an alternative to the first model (Thompson *et al.*, 1998) and the most used method for stock estimates in inland water (Gatz & Loar, 1988; Donkers *et al.*, 2012). The assumptions of this model are a closed population, random distribution and same catch probability between mark and unmarked individuals of the same species (White *et al.* 1982) and no mark loss. The mark-recapture model is generally used for abundance estimates in small lakes (Gresswell *et al.*, 1997) to great lakes (Dahm *et al.*, 1992; Donkers *et al.*, 2012). This model is more appropriate for low capture efficiency or low stock (Laurent & Lamarque, 1975).

Catches per unit effort (CPUE), instead of giving estimates densities, offer a view on proportional changes which occurred in an exploited fish population. Both CPUE and fish stock estimates are useful in understanding changes in fish stock (Peltonen *et al.*, 1999).

Collecting information about age and growth is important for understanding ecology and biology of any species. Age and growth rate are usually determined by using hard structure such as otoliths (Kwak *et al.*, 2006), bones (Alp *et al.*, 2011) or scales (Pompei *et al.*, 2011).

Growth rate information permits comparisons between different water bodies or different years but also the study of mortality rates or appreciates the general health of a population (Kwak *et al.*, 2006). In fisheries research and management, these aspects are very important.

Studies on long-term data sets are important to assess impact of one or more factors on organisms living in an ecosystem (Daufresne *et al.* 2003). Temperature and hydrology are factors which influence generally freshwater fauna (Poff *et al*. 1997). But invasive species can also affect fauna after their arrival in a new ecosystem (Phelps, 1994; Karatayev *et al.*, 1997; Pace *et al.*, 1998). For example, in the San Francisco Bay, invasion by the Asiatic clam *Pomatocorbicula amurensis* results in a decline in plankton (Alpine & Cloern, 1992; Kimmerer *et al.*, 1994) and plankton-feeding fish (Moyle *et al.*, 1991). Spread of invasive molluscs can also increase biomass of benthophage fish (Karatayev *et al.*, 1997).

In the River Meuse, 23 fish species were found during sampling by gillnetting and electrofishing from 1998 to 2000 (Goffaux *et al*. 2005). Other species, potentially invasive, are also found more and more frequently during sampling, for example Wels catfish *Silurus glanis*, Asp *Aspius aspuis* or Western Tubenose goby *Proterorhinus semilunaris*. The River Meuse has been recently colonized by Asiatic clams *Corbicula* spp. (Swinnen *et al.*, 1998) and dreissenids mussels (Marescaux *et al.* 2012).

Roach *Rutilus rutilus* (L., 1758) is one of the most commonly and widely distributed fish in European rivers (Kottelat & Freyhof, 2007). Roach is also important for recreational anglers. In 1993, roach stock in the River Meuse (Belgium) has been investigated by mark-recapture using the Jackson method. Its density was estimated at 3699 roach ha^{-1} (Didier & Micha, 1996). The study was continued in 2000 until 2002 and the density was comprised between 3035 and 3145 ha^{-1}, demonstrated a stable roach population (Evrard & Micha, 2003). Since this last study, according to indirect indicators, it seems that this stock has undergone a drastic decline. In the fish pass of Tailfer (lat. 50°24’1.29”N; long. 4°52’59.7”E), roach passages fluctuated between 7856 and 36983 per year in the beginning of the 1990s. Since 2006, roach passages are under 1500 during spring and summer. The lowest passage is obtained in 2013 with a maximum of 17 passages inventoried. A new investigation by mark-recapture confirms the decrease of roach stock with estimates of densities above 500 roach ha^{-1} (Latli & Kestemont, 2010).

The aim of the present study was to analyse data obtained in the River Meuse over the last 20 years. First, we compare historical and current estimates of roach stock in three reaches, Hastière, Tailfer and Visé. Estimates of density and biomass have been assessed by using the mark-recapture model. Secondly, an analysis of growth rate and mortality has been achieved by scale reading to see any impact of the decrease of stock on these population parameters. Thirdly, an analysis at larger scale was performed with fish pass data to seen any intrinsic population change with links to environmental (chlorophyll *a*, discharge, pH, oxygen saturation, phosphorus, ammonium, nitrite, temperature, suspended matter) and biological (Great cormorant populations) parameters. This approach allowed us to determine which

parameters are the most reliable to our problematic. Finally, fish assemblages were described by an analysis of biological and ecological fish traits.

Study area

The River Meuse is 905 km long and its total catchment area is 36 011 km². The river rises in Eastern France and flows throughout Belgium and The Netherlands before meeting the Lower Rhine and forming the Dutch delta. It debouches in the North Sea (Fig. 1) (Descy, 1987). The slope of the River Meuse is 0.23‰. In Belgium, the river looks like a bream zone as a consequence of heavily canalisation during the last 150 years. Fifteen dams have been erected on its course in Belgium which allow shipping of 1350 tons upstream Namur (Tans, 2000) and 9000 tons downstream Namur but disturb flow rate, migration of fish species and natural zonation patterns. Naturally, the river in Belgium is a barbel zone according to Huet's zonation (Micha & Pilette, 1988). Natural banks are relatively rare as a result of canalisation. A large description in long term changes in water temperature, discharge, suspended matter and orthophosphate can be found in Descy *et al.* (2009). During the study period at Tailfer, chlorophyll *a* ($\mu g.L^{-1}$) and zooplankton ($ind.L^{-1}$) have decreased. Soluble reactive phosphate ($mg\ P\ L^{-1}$) presents a slight decrease. Extinction coefficient (m^{-1}), related to phytoplankton biomass has increased (Pigneur *et al*. 2014).

The present study was carried on three different reaches in Belgium: Hastière, Tailfer and Visé, located 488, 518 and 611 km respectively from spring.

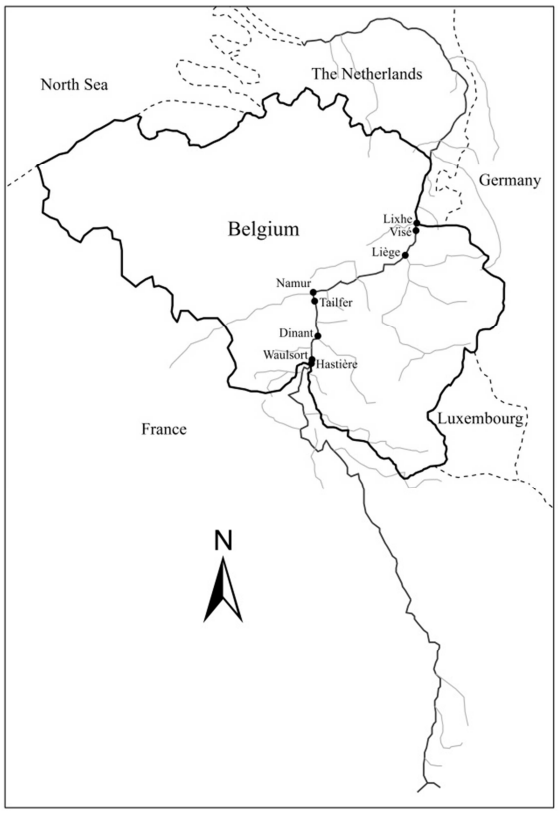


Fig. 1: Location of the River Meuse basin and the sampling sites

Materials and Methods

Fish sampling

Before estimation of roach stocks and their dynamics in two reaches of the River Meuse, 16000 roach grew in captivity were marked by clipping off the right pelvic fin on November 9th 2012 and restocked homogeneously in the 24 hours in the reaches of Hastière (7500 roach) and Visé (8500 roach). Sampling begun 4 days after restocking to let dispersal and mix with wild roach populations occurred.

During November 2012, 20 samples were taken from the River Meuse (12 by gillnetting and 8 by boat electrofishing). Four days of sampling were necessary on each reach. The samplings were taken at different sites during the study. In the reach of Hastière, 5 gillnet sampling and 5 electrofishing were done. In the reach of Visé, the balance between gill netting and electrofishing has not been respected because of low availability of bank less than 1.5 meter deep. In this reach, 7 gill nettings and 3 electrofishing were done. Gillnetting was performed with a set of 3 to 8 gillnets (length: 50 m; height: 2 m) with different mesh sizes (15, 20, 25, 30 and 40 millimetres). Gillnets were exposed in the main channel for 1 to 6 hours during daytime. At the same time, an electrofishing was carried out along shallow banks in an upstream direction. The generator consists in a 7 KW alternator delivering a continuous current (150 - 300 V at 3 A). The cathode was floating on the rear side of the boat. Three persons were used, one boat driver, one dip netter and one hand-held anode. After sampling, fishes were identified. Roach were measured to the nearest mm (Total length) with a measuring board and weighted to the nearest g individually. Identification as marked or unmarked roach was done by three persons for a correct reporting of marks.

Stocks estimates

The principle of the mark-recapture model is that the ratio of fish unmarked captured *n* to the total population *N* is the same as the ratio of fish marked captured *m* to the total fish marked *M* (Gatz & Loar, 1988). Estimates by the Petersen method were obtained using the following equation (Petersen 1896):

$$N = n * m/M \qquad (1)$$

Upper and lower confidence intervals (95%) were estimated with Poisson approximation to the hypergeometric distributions. Procedures assumed that the proportion of recapture fish is binomially distributed. Confidence limits are read off Poisson distribution frequency by entering observed number of recaptured fish *m*. Limits obtained are substituted for *m* in equation (1) and corresponding limits of *N* are calculated (Ricker, 1975).

Estimates have also been investigated with the Jackson's positive method (2) (Jackson, 1939). With this method, marking occurs on one occasion followed by multiple recaptures events (Begon M., 1979):

$$N_0 = r_0/q_0 \qquad (2)$$

Where q_0 = marked proportion of a hypothetical random sample taken on day *0*

r_0 = number of individuals marked and released on day *0*

Methods for estimating q_0 and confidence intervals of N_0 are reviewed in Begon (1979).

Estimate of biomass *B* is calculated by the formula (3) using *N* and its confidence limit (1 and 2):

$$B = N * \bar{P} \qquad (3)$$

Where $\bar{P}$ = Average weight

Capture per unit effort

In addition to stock estimates, stocks dynamics was also approached with gillnet catches per unit effort (CPUE). Even if CPUE doesn't reflect an estimate of density, it can show proportional changes in stocks (Peltonen *et al.*, 1999) and give additional information. Data from gillnets with mesh size 20 and 30 mm were used. CPUEs are reported in catch per square meter per 30 minutes of fishing effort.

Because of unequal size samples and variance heterogeneity, we used Welch statistic (Welch, 1951) to compare CPUEs. Multiple Welch paired-tests were performed to test significant differences between years in CPUEs with the same mesh size. Corrections for multiple paired-tests were assessed by sequentially rejective Bonferroni test (Holm, 1979).

Dynamics of roach populations

Age and growth rate were read from scales (Mann, 1973). Between 3 and 10 scales were collected from 56 specimens caught in each reach. Scales were taken above the lateral line up the dorsal fin. After removing mucus, scales were fixed on slides. Age reading was carried out independently by two persons. After age accordance, measures of radii (to the nearest mm) were carried out on the posterior field using a binocular. Total lengths at different ages were back-calculated using the Lee (1920) formula using measures of radii. Growth was described by the Von Bertalanffy growth curve (VBGC) model (Bertalanffy, 1938) described by the equation (4):

$$L_t = L_\infty * (1 - e^{-K*(t-t_0)}) \qquad (4)$$

Where L_t = Total length at age *t*

L_∞ = Asymptotic length or Maximal size

K = Growth coefficient

t_0 = Hypothetical age when length equal 0

The method of Ford-Walford was used to determine asymptotic length L_∞. Growth coefficient *K* and theoretical age t_0 were determined using the Von Bertalanffy method.

We used Ø' index of growth performance (Pauly & Munro, 1984; Naddafi *et al.*, 2005) calculated by formula (5) in order to compare growth of roach between years and sites:

$$\emptyset' = \ln(K) + 2 * \ln(L_\infty) \qquad (5)$$

The instantaneous rate of total mortality Z was estimated using length-converted age catch curve using the equation of Von Bertalanffy and by reporting age on the X-axis and natural logarithm of number of individuals by cohort on the Y-axis. The regression is equal to (6):

$$\ln(N_t) = a + b * t \qquad (6)$$

Total mortality *Z* is equal to -*b* (Ricker, 1975; Pauly, 1997).

Instantaneous rate of natural mortality *M* was estimated using the empirical equation of Pauly (1980) (7):

$$\log(M) = -0{,}0066 - 0{,}279 * \log(L_\infty) + 0{,}6543 * \log(K) + 0{,}4634 * \log(T) \qquad (7)$$

Where L_∞ and *K* are from the VBGC (4)

T = Mean annual water temperature (°C)

Instantaneous rate of fishing mortality *F* was calculated as the difference between instantaneous rates of total and natural mortality (8):

$$F = Z - M \qquad (8)$$

The ratio of instantaneous rate of fishing and total mortality was calculated to estimate exploitation *E* (9):

$$E = F/M \qquad (9)$$

Fish population analysis

For tracking the long term evolution of fish population, we follow two fish passes, at Tailfer dam on the middle Belgian Meuse and at Lixhe dam on the Lower Meuse. At Tailfer, fishes were captured with a trap for the following years: 1989 to 1994, 2006 and 2009 to 2011. Fourteen pools composed the fish pass (1.95 x 1.50 x 0.75 m) each dropping in elevation by (0.13 - 0.15 m). Discharge at the outlet is closed to 0.24 $m^3.s^{-1}$ and water velocity over the traverse is about 0,9 $m.s^{-1}$ (Prignon *et al.*, 1998). All fishes were counted except young of the year and common bleak (*Alburnus alburnus*) because of high abundance during the nineties. During migration peaks, fishes were collected each day. Outside migration period, the trap was checked two times a week. The trap placed in the upper pool of the pass had a shape of a cone at the entrance and a steel grid (1 cm wide between bars) at the exit.

Lixhe dam has two fish passes put into operation in 1980 and 1998. The older is a pool and weir pass of 48 m length composed of 56 pools (1.5 x 0.9 x 0.4 m) with 2 cones trap at the upper pool. The new one is a pool and vertical slot pass of 305 m length composed of 26 pools (1.4 x 1.1 x 1.5 m) with a cage at the upper pool. The mean discharge was respectively 0.135 and 1.0 $m.s^{-1}$. We have followed the 2 fish passes from 1999 to 2012. During migration peaks, fishes were collected each day and all fishes were counted except young of the year.

Species abundance was expressed as CPUE. For each year, we divided fish abundance by the period of sampling (in month). We excluded of the analysis two introduced species (Brook trout *Salvelinus fontinalis* and Rainbow trout *Oncorhynchus mykiss*) and species accounting for less than 5% of the total fish sampled.

We used 8 physical and chemical parameters (oxygen saturation, ammonium, nitrite, phosphorus, water temperature, chlorophyll *a*, pH and discharge) collected monthly close to fish pass by the Environment and Water Department of the Public Service of Wallonia. We included in our study one biological variable: the number of Great Cormorant attending during winter in the same reach of our sampling sites.

We used three kinds of approaches for processing data. First, a redundancy analysis (RDA) was carried out to compare relationships between faunal changes and environment variables (R-software package Vegan). We standardized the environmental variables and transformed abundances with square roots or Hellinger method (Oksanen *et al.*, 2013). We used a permutation test (package Packfor) in an aim to identify explanatory variables which were significantly correlated with fish populations (Dray *et al.* 2007). Next, we applied a cluster analysis based on site coordinates of the two first factorial axes of the RDA with a Ward's linkage algorithm (Ward 1963) in order to assemble site samples in larger groups with similar characteristics. Secondly, we compared total CPUE, CPUE per taxa association, diversity, and Shannon index of the different groups determined previously with the clustering. We used a one-factor MANOVA for improved significance. Third, we studied biological and ecological fish traits with a Fuzzy Principal Component Analysis (Chevenet *et al*. 1994). Traits which are uninteresting for our study or redundant were excluded. Finally, we selected 3 biological and ecological traits (Feeding habitat, Feeding diet, Number of oocytes / g of fish and Number of spawning events) divided into 10 modalities binary coded from Buisson & Grenouillet (2009). Fish assemblages were described by crossing fish proportions and their affinity for each modality.

Results

Density estimates

A total of 462 roach unmarked were caught by electrofishing and gillnet in the reach of Visé. Gillnet catches represent 99.8% of capture. On 8500 roach marked, 71 have been recaptured during the sampling period. Recapture percentage is 0.84%. Most of recapture are due to gillnet sampling, whether 90% of all recapture. On the reach of Hastière, a total of 241 roach unmarked have been caught, mostly by gillnet sampling. Recapture percentage is 3.75%. Most of recapture are due to electrofishing (62%) along banks. The highest recapture percentage is found in the reach of Hastière.

Abundances of roach in the River Meuse have been investigated by mark-recapture method. As seen in Table 1 and Table 2, a decrease in estimated densities in the reach of Tailfer is detected. Between 1993 and 2002, roach stock appeared constant. Its density was comprised between 10426 (8935-12166) and 4341 (3668-5138) roach ha^{-1} according to Petersen method

and between 3699 (2556-5352) and 3035 (2157-3805) according to Jackson method. Estimates conducted in 2001 and 2002 tend to highlight a decrease according to Petersen method in this reach although estimates by Jackson method reveal a steady stock (data for 2001 not presented). More, CPUEs obtained between 1993 and 2002 from gillnet with mesh size of 20 and 30 mm show no significant difference (Fig. 1). In 2010 and 2011, a new study was conducted on the reach of Tailfer and its conclusions are that roach stock has undergone a drastic decrease in less than 10 years. Both methods give approximately the same results. Even if no historical data exists on reaches Hastière and Visé, roach stocks appeared close to results obtained in the reach of Tailfer between 2010 and 2011. Petersen estimates conducted to a density of 240 (191-303) roach ha^{-1} in the reach of Visé and a density of 140 (125-158) in the reach of Hastière (Table 1). According to Jackson estimates, density in the reach of Visé is 233 (212-256) roach ha^{-1} and 127 (70-230) in the reach of Hastière. Estimates approached by the two methods show similar results for years 2010 and 2012.

Table 1: Summary of Petersen estimates and resulted density and biomass obtained

Year	Site	Area (ha)	Recapture rate (%)	*M*	Catch		*N*	Density (roach ha^{-1})			Biomass (kg ha^{-1})			Size class
					n	*m*		Lower 95%	Mean	Upper 95%	Lower 95%	Mean	Upper 95%	
1993	Tailfer	76.4	1.73	9315	13768	161	796577	8935	10426	12166	480.9	561.2	654.8	91-310
2000	Tailfer	76.4	2.16	10442	17997	226	831528	9554	10884	12399	575.1	655.2	746.3	51-370
2001	Tailfer	76.4	0.65	15450	2822	101	431682	4650	5650	6865	280.2	340.5	413.7	61-300
2002	Tailfer	76.4	1.31	10300	4347	135	331660	3668	4341	5138	220.8	261.3	309.3	51-370
2010	Tailfer	76.4	2.20	10100	761	222	34622	397	453	517	8.8	10.0	11.4	91-340
2011	Tailfer	76.4	1.04	10000	303	104	29135	315	381	462	19.5	23.6	28.6	61-290
2012	Visé	230.0	0.84	8500	462	71	55310	191	240	303	12.5	15.8	19.9	121-330
2012	Hastière	45.8	3.75	7500	241	281	6432	125	141	158	9.0	10.2	11.4	61-340

Table 2: Summary of Jackson estimates and resulted density and biomass obtained

Year	Site	N_0	Density (roach ha^{-1})			Biomass (kg ha^{-1})			Size class
			Lower 95%	Mean	Upper 95%	Lower 95%	Mean	Upper 95%	
1993	Tailfer	282599	2556	3699	5352	137.6	199.1	288.0	91-310
2000	Tailfer	240248	2021	3145	4892	121.7	189.3	294.5	50-370
2002	Tailfer	231863	2157	3035	3805	137.1	182.6	230.5	51-370
2010	Tailfer	36159	380	473	590	8.5	10.6	13.2	91-340
2011	Tailfer	11412	91	149	245	5.7	9.3	15.2	60-290
2012	Visé	53617	212	233	256	13.9	15.3	16.8	121-330
2012	Hastière	5799	70	127	230	5.0	9.2	16.6	61-340

Capture per unit effort

Values and confidence intervals (95%) of CPUEs are shown in figure 2. CPUEs obtained in 2012 on both sites are not different (p = 0.27 for gillnet of 20 mm and p = 0.96 for gillnet of 30 mm). CPUEs in 2012 for gillnet with mesh size of 20 mm are highly different from 2000 and 2002 (p <0.01) but not different for CPUEs from 1993 and 2001 (p >0.06) after correction with sequentially rejective Bonferroni test. CPUEs in 2012 for gillnet of 30 mm are highly different from 2000, 2001 and 2002 (p <0.001) but not from 1993 (p = 0.40 and 0.46). CPUEs values for gillnet of 20 mm of 1993, 2000, 2001 and 2002 are not different (p >0.07). Comparison of gillnet of 30 mm for years 1993, 2000, 2001 and 2002 gives the same result (p >0.40).

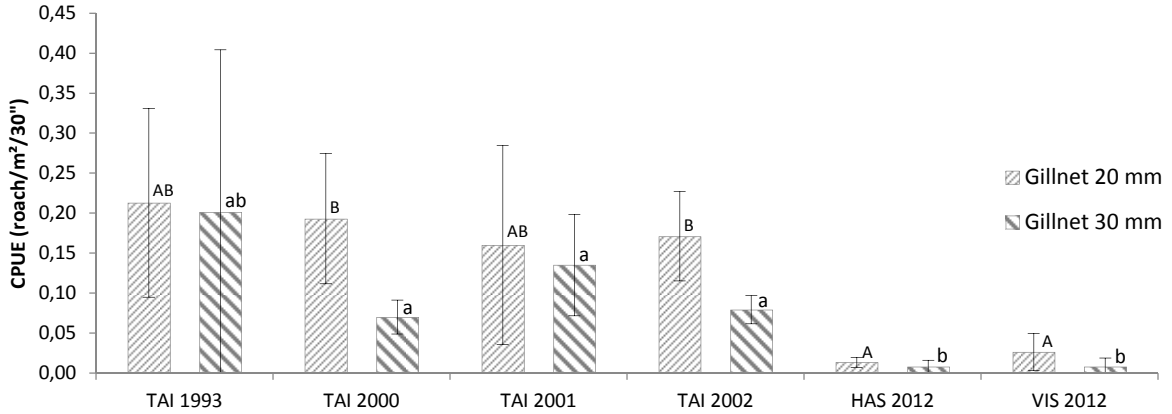


Fig. 2: CPUE for gillnet 20 and 30 mm obtained in the reaches of Tailfer (TAI), Hastière (HAS) and Visé (VIS), confidence interval of 95%

Dynamics of roach populations

VBGC for roach in the River Meuse are given in figure 3. The parameters of the VBGC fitted to mean back-calculated TLs at age and performance index Ø' are shown in Table 3. It appears that roach populations in the reaches of Hastière and Visé have a growth *K* comprised between those estimated for the reach of Tailfer (0.12 to 0.22). Asymptotic lengths L_∞ estimated in 2012 are close to those estimated between 1989 and 2002 but higher than in 2010 and 2011 (Fig. 3; Table 3). For the reach of Tailfer, asymptotic length tends to decrease between estimates of 2010/11 and 1993/2002 while growth stays stable. Growth performance index Ø' reveals a low variability between estimates. The highest value is found in the reach of Visé and Hastière.

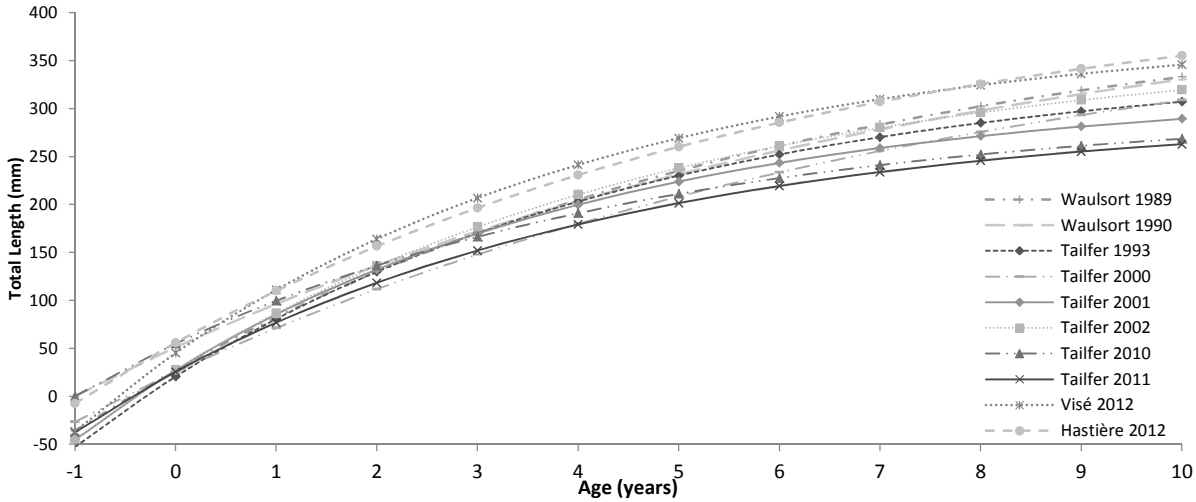


Fig. 3: Von Bertalanffy growth curves obtained for different roach stocks in the River Meuse

Table 3: Growth parameters of VBGC, performance index (Ø'), mortalities and exploitation of roach

Sites	Year	L_∞	K	t_0	Ø'	Z	M	F	E
Waulsort	1989	421	0.15	-0.5	10.2				
Waulsort	1990	451	0.12	-1.0	10.1				
Tailfer	1993	352	0.20	-0.3	10.1	0.71	0.40	0.31	0.43
Tailfer	2000	431	0.12	-0.5	10.0				
Tailfer	2001	322	0.22	-0.4	10.0				
Tailfer	2002	371	0.19	-0.4	10.2				
Tailfer	2000 - 2002	368	0.18	-0.4	10.1	0.69	0.38	0.31	0.45
Tailfer	2010	302	0.20	-1.0	9.8	0.92	0.45	0.47	0.51
Tailfer	2011	316	0.18	-0.6	9.8	0.60	0.40	0.20	0.33
Hastière	2012	438	0.15	-0.8	10.3	0.82	0.33	0.49	0.60
Visé	2012	385	0.21	-0.6	10.3	0.78	0.45	0.33	0.42

Mortality rates and exploitation are given in Table 3. Values of total, natural and fishing mortalities are relatively stables through years but current mortalities are slightly higher than historical data. Exploitation, which reflects all types of mortalities, is high in the reach of Hastière. In the reach of Visé, exploitation is lower and comprised between estimates for the reach of Tailfer.

Fish population analysis

Tailfer pass - During the last twenty years, we observed an impressive modification of the fish population in the River Meuse. Some species which overlooked population in the past appeared now only occasionally. From 1989 to 1994, a mean of 2283±1403 fishes per month were captured at Tailfer. During last years, we noticed a significantly decrease (p = 0.01) with 441±413 catches (Fig. 4). Diversity follow the same trend, with a significantly decrease of 30% (p = 0.001). On the other hand, equitability (Shannon index) increases slightly but not significantly.

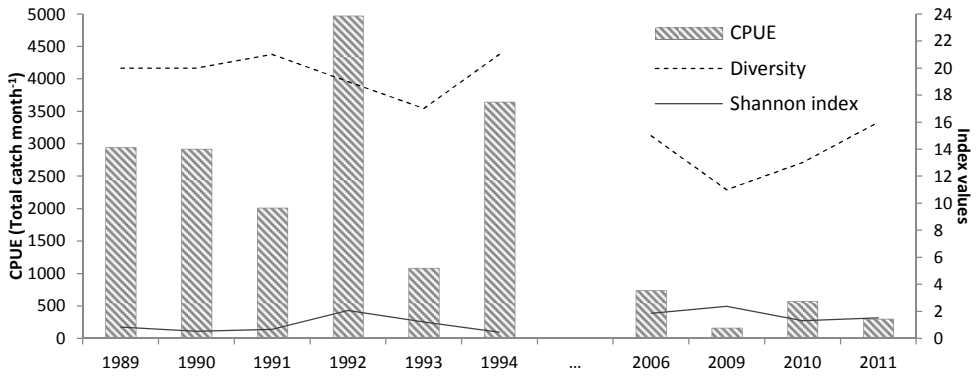


Fig. 4: Evolution of the mean annual fish caught at the Tailfer pass

The first two axes of the RDA explain 66% and 18% of the total variation respectively in the data set. The temporal evolution was strongly correlated with the first axis of the RDA (Fig. 5a) and we could identify two groups of sites on the factorial map confirmed by the clustering on the RDA axe (Fig. 5b). At the bottom left, we find the sites sampled before 1994 (group 1)

and at the top right the sites sampled after 2006 (group 2). The first group is more compact than the second one which tells us that fish population was more similar in the past than actually. If we analyse environmental variables, group 1 is more correlated with a high concentration of chlorophyll *a*, discharge and phosphorus concentration. At the opposite, group 2 benefits from a higher density of Great Cormorant, pH, oxygenation and temperature.

Secondly, we could observed that a lot of species are close of the origin of the first axe, which means that just a few species could explain the "year" repartition. So, roach are greatly correlated with group 1, and to a lesser extent eels (*Anguilla anguilla*), silver bream (*Blicca bjoerkna*), common barbel (*Barbus barbus*) and dace. On the other hand, group 2 is correlated with gudgeon (*Gobio gobio*), chub (*Squalus cephalus*) and minnow (*Phoxinus phoxinus*).

The permutation test realized on the environment data indicated that only the concentration of chlorophyll *a* is significantly correlated with fish data ($p = 0.013$).

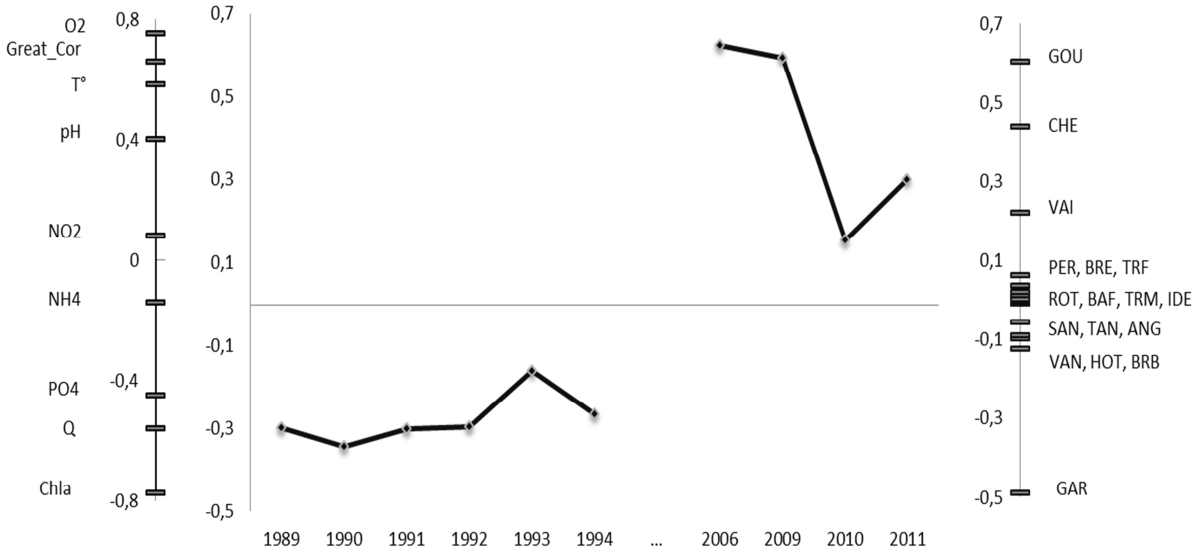


Fig. 5a: Time series of site scores on the first axis of the redundancy analysis of fish data (RDA1=66%). Contribution of taxa (at the right) and environmental data (at the left) on the first axis of the redundancy analysis. (ABL, common bleak; ANG, eel; BAF, common barbel; BRB, silver bream; BRE, common bream; CCO, common carp; CHE, chub; GAR, roach; GOU, gudgeon; HOT, common nase; IDE, ide; PER, perch; ROT, rudd; SAN, pikeperch; TRF, brown trout; VAI, minnow; VAN, dace) (Chla, chlorophyll a; T°, temperature; Q, discharge; Great Cor, Great cormorant; O2, oxygen saturation; NH4, ammonium, NO2, nitrite; PO4, phosphorus, pH).

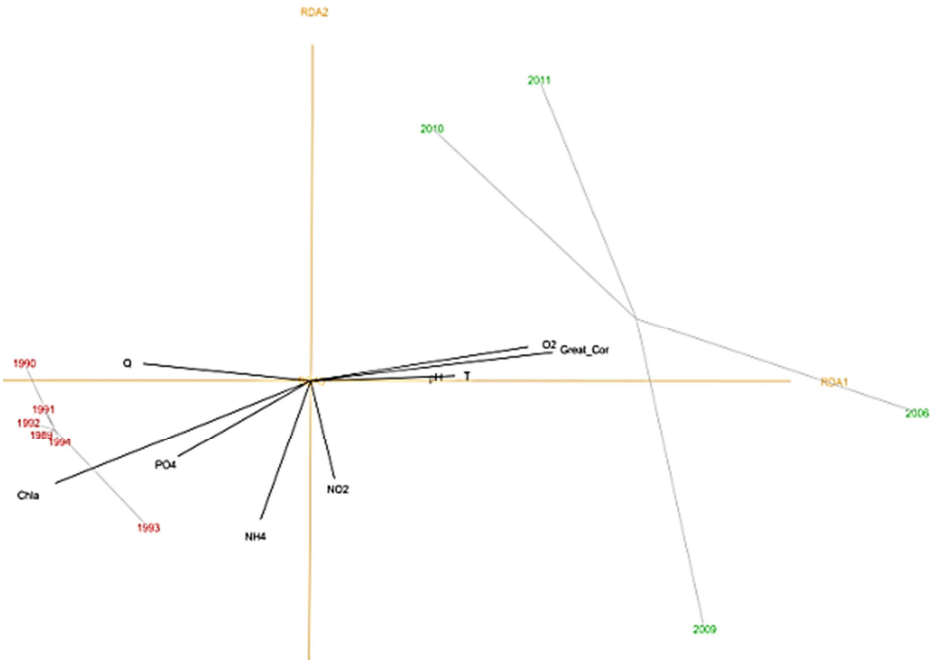


Fig. 5b: Clustering on the RDA axes with centroids of the two groups (group 1 in red and group 2 in green). Environmental variables are represented by yellow line.

All species present before 1994 saw their population decrease after 2006 except for minnow, gudgeon and chub. Species which endured the most important decrease (p = 0.001) were the limnophile cyprinids living in the water column like roach, dace (*Leuciscus leuciscus*) and rudd (*Scardinius erythrophtalmus*). For example, CPUE for roach dropped from 1950±1208 to 179±222 between the two study periods. Salmonidae and benthic rheophilic cyprinid also saw their populations decreasing (respectively p = 0.01 and 0.05).

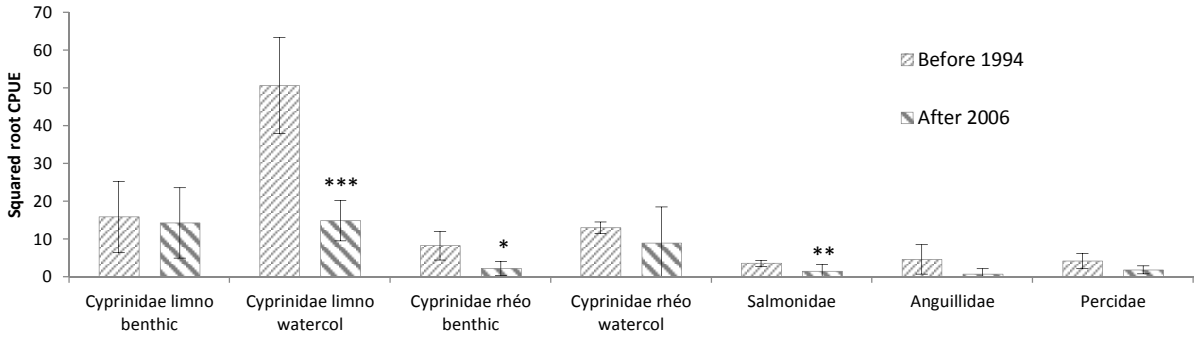


Fig. 6: Comparison of squared root transformed CPUE per taxa association of the monitoring of the Tailfer pass, * 0.5%, ** 0.01%, *** 0.001%

The fuzzy principal component analysis (FPCA, Chevenet *et al.* 1994) explains 82.8% of the variation on the first axe and 14.3% on the second axe. The figure 7 clearly illustrates the change in community structure along a temporal gradient on the first axis of the FPCA. Once more the group 2 is more variable on the FPCA than the first group. The feeding habitat and the feeding diet were strongly correlated with the temporal gradient. Group 1 comprises omnivorous fish which found mostly their food in the water column contrary to group 2 with

benthivorous and invertivorous fish. The proportion of carnivore seems unchanged between the two periods. Fish linked to group 1 were preferentially monovoltin with a lot of oocyte by female, in contrast to group 2 fishes which spawned less eggs several time a year.

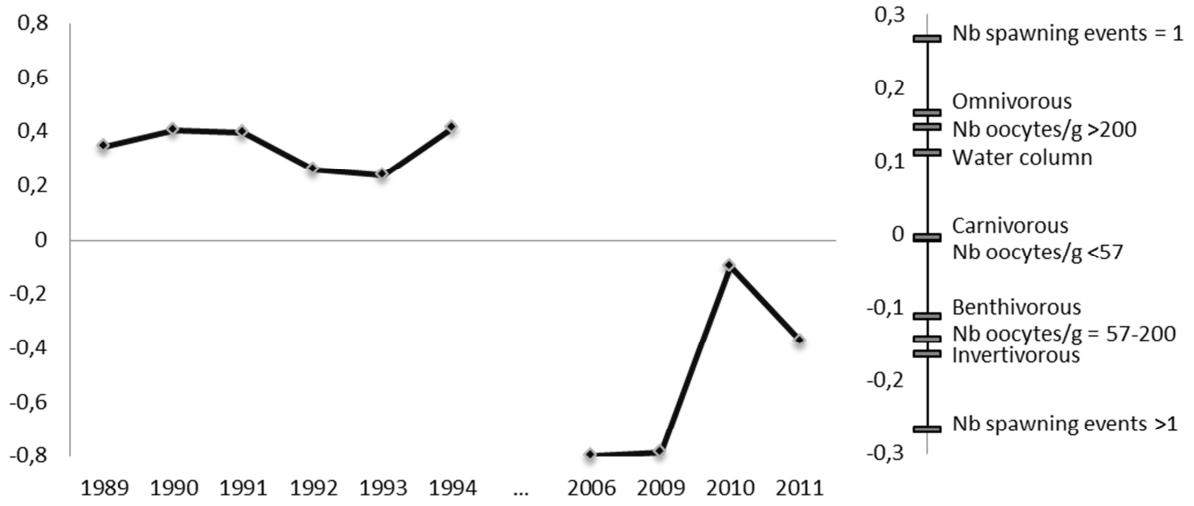


Fig. 7: Time series of site scores on the first axis of the Fuzzy Principal Component Analysis of fish data (FPCA1=82,8%). Contribution of 10 modalities applied for 4 biological traits on the first factorial plane (at the right) on the first axis of the FPCA.

Lixhe pass - At Lixhe pass, number of capture was divided by two between period pre/post 2000 and by three between period pre/post 2006 (Fig. 8). During the first period, 1437±185 fishes were counted each month, less than 596±117 during the second period and 222±56 during the last period. By contrast, diversity and Shannon index were relatively stable over time with a mean of 21.2 species inventoried each year.

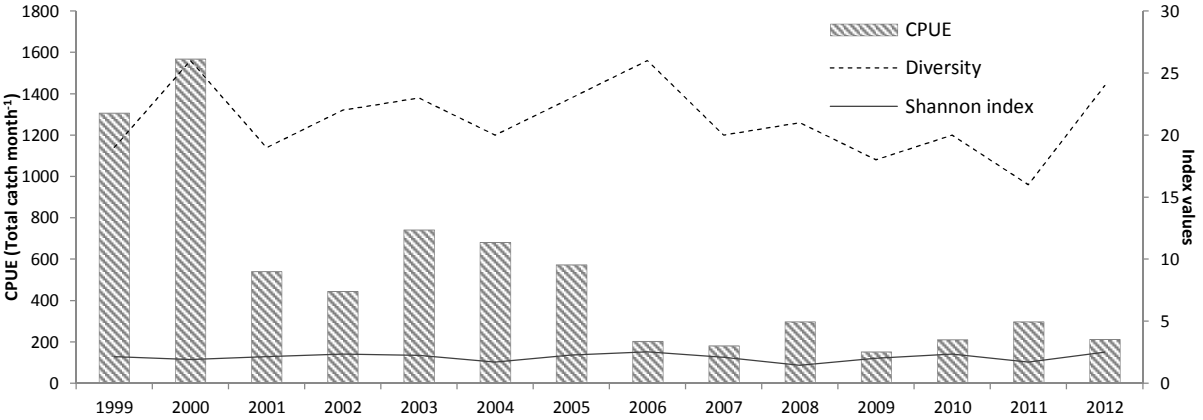


Fig. 8: Evolution of the mean annual fish caught at the Lixhe pass.

Axes of the RDA explain respectively 59 and 28% of the total variation in the data set. The figure 9b classifies data into 3 different groups, group 1 gathered years 1999 and 2000, group 2 years 2001 to 2005 and 2008, group 3 years 2007 to 2012. Along X-axis, we could observe a clear temporal gradient with the historical years at the left and the recent years at the right. On the X-axis, year 2008 was really close to group 3 than group 2 so we decided to gather years from 2007 to 2012 in the groups 3.

Three species (common bleak, roach and eel) were strongly correlated with groups 1 and to a lesser extend with group 2, a sign of decrease for these species with time (Fig. 9a). Silver and common bream were more correlated with group 2 than other group. Other species were located close to the axes origin because their population didn't significantly change during the study period. Five environment variables were correlated with the first RDA axe. Great cormorant, chlorophyll a, temperature and phosphorus seem more large before 2006 and ammonium concentration increase over time. Other environment variables were more correlated with Y-axis which wasn't made a clear tendency. However, the permutation test realized on the environment data indicated that only the number of wintering Great cormorant was significantly correlated with fish data ($p = 0.0261$).

CPUE decrease significantly between groups over time ($p = 0.001$). Species most impacted are common bleak (23.3±5.8, 11.8±5.1 and 3.0±1.0), roach (20.1±0.5, 10.2±4.4 and 4.5±1.8) and eel (17.8±1.5, 10.8±4.7 and 7.8±3.0). One more time, group of species which endured the most important decrease ($p = 0.001$) were limnophile cyprinids living in the water column, benthic limnophile cyprinids ($p = 0.05$) and anguillidae ($p = 0.05$) (Fig. 10).

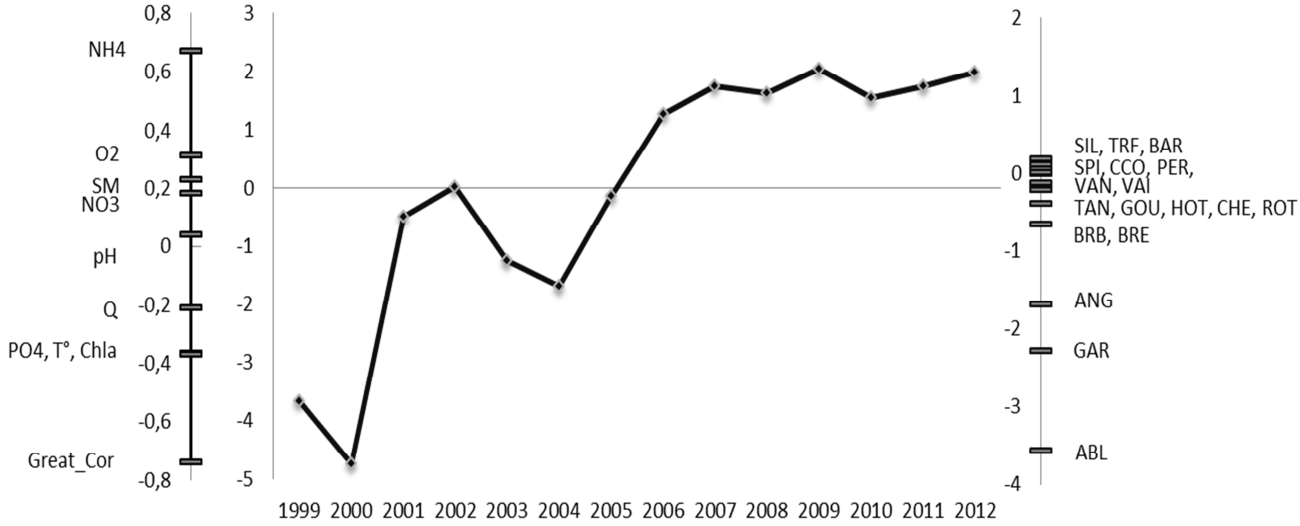


Fig. 9a: Time series of site scores on the first axis of the redundancy analysis of fish data (RDA1=59%). Contribution of taxa (at the right) and environmental data (at the left) on the first axis of the redundancy analysis. (ABL, common bleak; ANG, eel; BAF, common barbel; BRB, silver bream; BRE, common bream; CCO, common carp; CHE, chub; GAR, roach; GOU, gudgeon; HOT, common nase; PER, perch; ROT, rudd; SAN, pikeperch; SIL, wels catfish; SPI, bleak; TAN, tench; TRF, brown trout; VAI, minnow; VAN, dace).

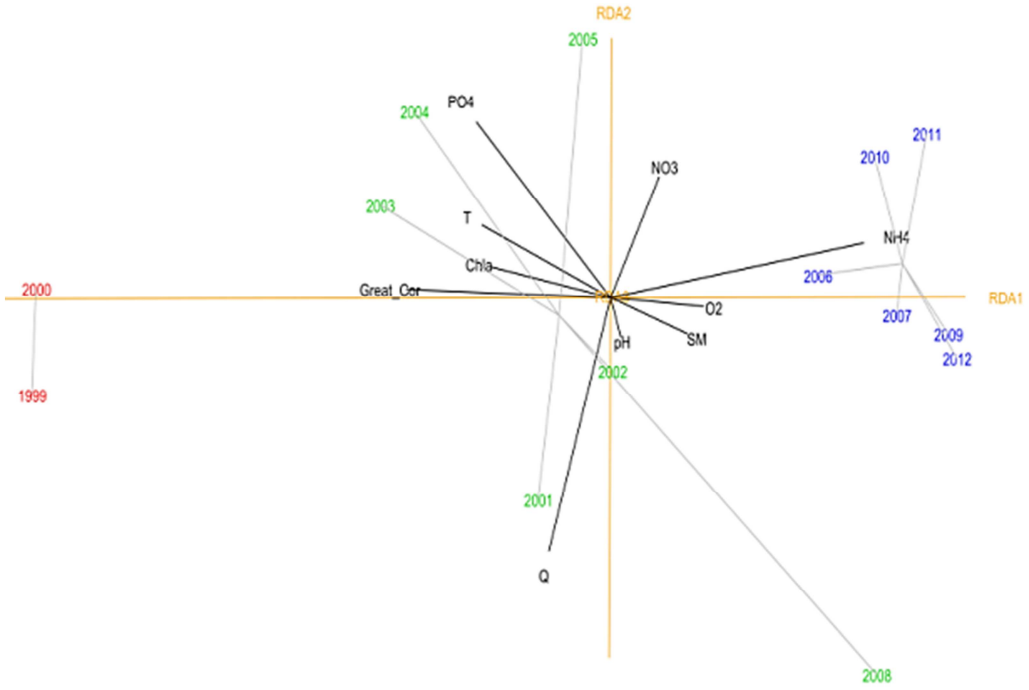


Fig. 9b: Clustering on the RDA axes with centroids of the 4 groups (group 1 in red, group 2 in green, group 3 in blue sky and group 4 in deep blue). Environmental variables are represented by yellow line.

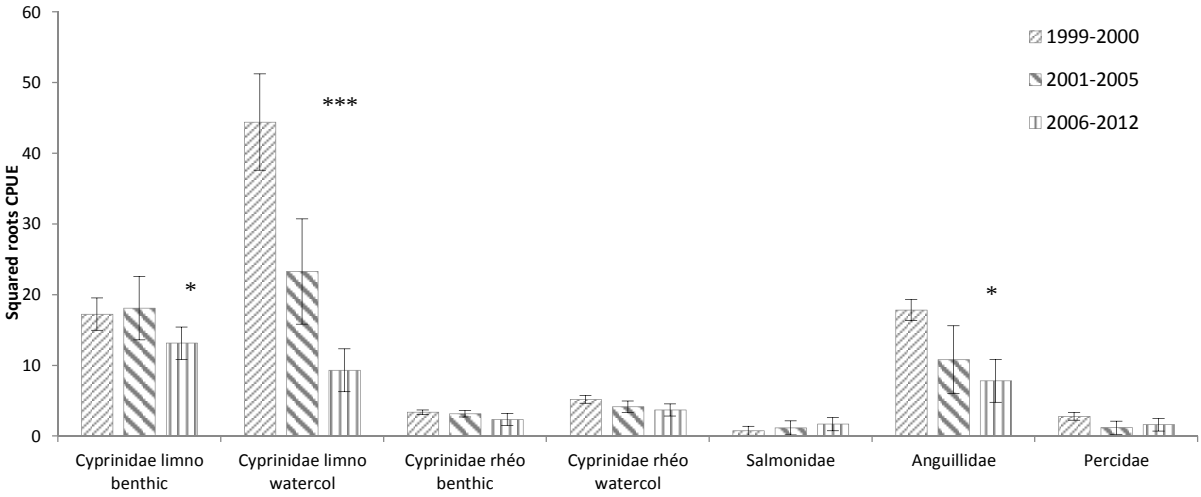


Fig. 10: Comparison of squared root transformed CPUE per taxa association of the monitoring of the Lixhe pass, * 0.5%, *** 0.001%

The fuzzy principal component analysis explains 52.4% of the variation on the first axis and 30.2% on the second axis. The temporal changing clearly appears in the figure 11, and we can identify the same temporal evolution and grouping than in figure 9a and 9b. Opposite to the Tailfer pass, Lixhe fishes were preferentially omnivorous and benthivorous during the beginning of the 2000 but found their food nowadays in the water column. The proportion of invertivorous doesn't change between the different periods but the presence of carnivorous increases over time. Fishes were preferentially multivoltin during the beginning of the 2000 and monovoltin for the last years.

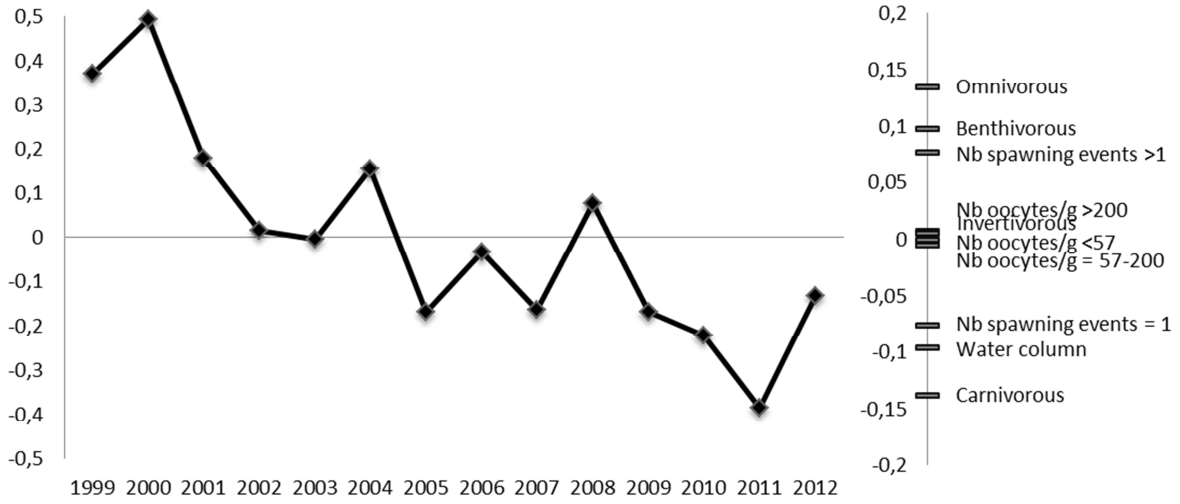


Fig. 11: Time series of site scores on the first axis of the Fuzzy Principal Component Analysis of fish data (FPCA1=52,4%). Contribution of 10 modalities applied for 4 biological traits on the first factorial plane (at the right) on the first axis of the FPCA.

Discussion

Estimates of roach density

Choice of mark-recapture method instead of removal method was due to high complexity for applying removal method in the River Meuse, which is a large (> 100m) and deep river (> 2m). Keslo and Shuter (1989) doubt the efficiency of removal method for lake populations. For these populations, the mark-recapture is the most used method for estimates (Gresswell *et al.*, 1997; Donkers *et al.*, 2012). The method of Petersen also called Lincoln Index is the simplest method to investigate a population (Begon M., 1979). This method often requires polling of multiple catch effort which can hide biases of each catch effort (Donkers *et al.* 2011). Jackson method is more adapted for our sampling protocol. Following the need of a large assistance for tagging, roach were marked on a single day. This single mass-marking was followed by multiple recaptures events by a trained team. These two aspects make the use of the Jackson's positive method efficient and extremely useful. This method is an extension of the Petersen method which allows loss but no gain (Begon 1979).

To meet mark-recapture general assumptions, marking and recapture periods must be short (Krebs 1999 in Donkers *et al.* 2011). In the present study, marking has been done on a single day and sampling was completed within 4 days on each reach less than a week after dumping of marked roach. This short period of time reduce violations due to emigration and immigration. It's assumed that no growth neither recruitment occurred during the sampling period (Ricker 1975). The closed population assumption appears to be met by dams delimiting each reach. Further, estimates have been conducted out the reproductive migration period during which roach migrate in an upstream direction for reproduction through fish passes. The assumptions of zero tag loss were addressed by fin clipping and correct reporting of mark by the use of three observers. Fin clipping was chosen for its facility and rapidity of tagging and because of non-regeneration possible during the short period of sampling. Short period of time between tagging and sampling should have reduced probability of unequal

mortality among unmarked and marked roach (Gresswell *et al*. 1997). We assumed an equal capture probability between marked and unmarked roach. We have chosen roach grew in captivity for tagging. It's the only possibility to mark a large number of fish in a short period of time (one day). It was impossible to catch sufficient wild roach in the River Meuse to mark them. More, the most efficient technic to catch roach is gillnetting sampling. But this technic is relatively destructive which brings the question on the survival rate after being released. The choice we made is without any behavioural biases as seen in the reach of Hastière where a lot of marked roach stayed hidden in aquatic vegetation more present in this reach which can lead to underestimate the natural population by increasing marked fish capture. Recapture rate in this reach is the highest in this study. More, these roach can suffer higher mortality compared with wild fish of the same age (Philippart, 1995; Brown & Laland, 2001).

Our results indicated that abundance estimates by mark-recapture methods of roach in the River Meuse are very low compared with historical data. In the reaches of Hastière, Tailfer and Visé, current estimates are below 500 roach ha^{-1} according to both methods. The lowest density is found in the reach of Hastière with 127 roach ha^{-1}. According to previous estimates in the reach of Tailfer, roach population was estimated to be comprised between 4000 and 10000 roach ha^{-1} according to the Petersen method. These estimates have been confirmed with the Jackson method which revealed a density relatively stable comprised between 3000 and 3700 roach ha^{-1}. Decline trend according to Petersen estimates is not highlighted with Jackson estimates which corroborate best field observations and experimental protocol. According to field observations, estimates by Petersen method in 1993 until 2002 overestimate roach density in the reach of Tailfer (Evrard & Micha, 2003).

In the River Thames (England), roach stock has been investigated by 'mark-recapture' by Williams (1965) and its density was estimated at 10000 roach ha^{-1} for roach over 10 cm fork length. In Lake Tjeukemeer (The Netherlands), roach density was estimated to be 585 roach ha^{-1}. This low density was attributed to scarcity of zoobenthos and competition from other species (Goldspink, 1979). In Lake Årungen, a eutrophic lake in Norway, biomass of roach was 550 kg ha^{-1} in the 1980s (Eie & Borgstørm, 1981). These estimates strengthen the abundance of roach in eutrophic environment. Eutrophication can have profound effects on fish communities, with cyprinid fishes such as roach dominating communities in these environments (Willemsen, 1980; Winfield, 1991). Roach is considered as a trophic generalist whom can use a large range of food from detritus to zooplankton, macrophytes and benthic macroinvertebrates (Hayden *et al.*, 2014). The River Meuse is a eutrophic river that corroborates with the high density of roach found in the 1990s and beginning of 2000s. Nutrients concentrations show no sharp decrease during the study period (Pigneur et al. 2014) which can explain the decline in fish stocks.

Gillnet CPUE has been widely used as an important parameter in monitoring abundance changes or like an index of fish abundance (Olin *et al.*, 2002, 2009; Mehner *et al.*, 2005). Statistical comparisons of CPUEs corroborate previous results for estimated densities. CPUEs obtained in 2012 by gillnet are significantly lower than those obtained in previous studies

expect 1993 (gillnets 20 and 30 mm) and 2001 (gillnet 20 mm). CPUEs for 2010 and 2011 (data not presented) have the same order of magnitude than 2012. As roach stocks are low, CPUEs are low to.

Growth and mortality of roach

Growth can be considered to be normal for roach in the reaches of Hastière and Visé. The parameter *K* which describe growth rate of the Von Bertalanffy growth curve is 0.15 and 0.21 $year^{-1}$ in the reach of Hastière and Visé respectively, in line with past estimates in the reaches of Tailfer and Waulsort. In other countries, growth rate of roach are 0.11 (for female) and 0.19 $year^{-1}$ (for male) in Lake Sapanca (Turkey) (Okgerman *et al.*, 2009), between 0.13 and 0.27 $year^{-1}$ in River Warta (Poland) (Przybylski, 1996), 0.29 $year^{-1}$ in Lake Maggiore (Volta & Jepsen, 2008), 0.24 $year^{-1}$ in Lake Piediluco (Giannetto *et al.*, 2014) (Italy), 0.21 $year^{-1}$ in Lake Geneva (France) (Ponton & Gerdeaux, 1987) and 0.30 $year^{-1}$ in Lake Lugano (Switzerland) (Guthruf, 2002). Regarding asymptotic length, populations examined in the present study show maximal lengths of 438 and 385 mm which are comprised between estimates in Tailfer and Waulsort. In other countries, our values are greater than estimates in the Netherlands (206.5 mm) (Goldspink, 1979) or Italy (357.5 mm) (Volta & Jepsen, 2008), around estimates in Turkey (318 and 472 mm) (Okgerman *et al.*, 2009) and England (425 mm) (Wyatt, 1988) and smaller than estimate in Lake Piediluco (478 mm) (Giannetto *et al.*, 2014). In the study of Lappalainen *et al*. (2008), regarding to latitude, our estimates of growth rate and theoretical length are comprised between values reported. The Ø' values are 10.3 on both sites, slightly greater than values reported in previous estimates in Tailfer and Waulsort. Values reported in literature, are 10.5 (Volta & Jepsen, 2008), 10.9 (Giannetto *et al.*, 2014), 10.1 (Ponton & Gerdeaux, 1987), 10.6 (Guthruf, 2002) for Europe, 9.9 to 10.1 for Turkey (Okgerman *et al.*, 2009). The obtained Ø' values of roach are very close to reported values from other countries.

Assumptions of the method used for estimating total mortality *Z* are a constant mortality for all ages considered for the evaluation, a great sample which recovered a maximum of cohort, each cohort must be recruited in equal quantities and until a critic length, vulnerability of each group to capture is constant (Pauly, 1997). First and second assumptions can be considered as respected. Populations of roach in the reaches of Hastière and Visé exhibit relatively constant total mortality over the entire range of ages sampled which is reflected by a high coefficient of determination (r^2= 0.96 for Hastière and r^2= 0.92 for Visé). For the evaluation of *Z*, 8 and 7 cohorts have been used for roach stock in the reach of Visé and Hastière respectively. Third and fourth assumptions have been respected by rejecting of the analysis cohorts which have been under estimated following a low sampling effort due to gears used. Current estimates of total mortality (0.78 to 0.82 $year^{-1}$) seem higher than past estimates (0.69 to 0.71 $year^{-1}$).

In an exploited stock, natural mortality is the most difficult parameter to estimate but is important for models of stock management. *A priori*, this mortality must be estimated in unexploited stocks (Pauly 1997). Following exploitation of stocks and insufficient catch curve, we used the equation developed by Pauly (1980) to estimate natural mortality. Natural

mortality in the present study is very close to previous estimates in the reach of Tailfer. Fishing mortality is high in roach stock of Hastière, leading to an over exploitation (60%). In the reach of Visé, exploitation is similar to past estimates. In the reach of Tailfer, exploitation stays constant between 1993 and 2002. A slightly increased is revealed in 2010. In 2011, exploitation is low (33%).

Fish population analysis

Although fish pass is an indirect selective fish inventory method, inherently unique, it is an important tool in management to control fish population (Roscoe & Hinch, 2010). Furthermore, in great river, there is no method which can offer a perfect sample of fish fauna. Electrofishing and gillnetting have their own limits (Casselman *et al.*, 1990; Pusey *et al.*, 1998). In order to have a better evaluation of great river fishes, we should use a combination of different technics (Goffaux *et al.* 2005). In our case, we can assert that fish pass capture was a good estimation of fish population from the River Meuse. This affirmation is right for cyprinids at less because roach stocks estimates realized previously on with other methods flaunted the same trend.

In the Belgian part of the River Meuse, we observed since the beginning of the 21th century a decrease in fish populations with a reduction of capture at fishes pass upper to 80%. Over the last ten years at Lixhe for example, mean fishes captured each month decrease from 1437 to 222 (Fig. 8). Almost of the species followed this trend, except exogenous species like asp and wels catfish. At Lixhe pass, study duration was sufficiently continuous to allows us to precisely visualize the two decrease periods, in 2000 for the first and 2006 for the second one (Fig. 8). However, we don't have earlier data that we could use as fish population reference before arrival of invasive molluscs and Great cormorant. At Tailfer pass, we have older data but intermediate data missed to allow us to situate accurately the decreasing period (Fig. 4). Although study time periods and typology were not analogous between Lixhe and Tailfer pass, tendency was similar which implies that fish changes concerned all the Belgian part of the River Meuse.

Species mostly impacted are the limnophilic cyprinids living in the water column like roach, dace and rudd but also the benthic rheophilic cyprinids like common barbel and common nase (*Chondrostoma nasus*). All those species had a zooplanktonic diet during early stage of their ontogeny (Nunn *et al.* 2007; Dettmers *et al.* 2001). That's why we can preferentially incriminate the decrease of zooplankton in the Meuse River (related with rarefaction of phytoplankton due to *Corbicula* spp. invasion according to Pigneur *et al.* 2014) as a probable cause of decline. Moreover, at Tailfer pass there is a significantly correlated link ($p = 0.0134$) between decrease of chlorophyll *a* concentration and fish fauna evolution (Fig. 5a). Feeding habitat trait (Fig. 7) presents a similar tendency with the second group of fishes which fed preferentially on the benthos contrary to the first group which found their food in the water column. Increase of water clarity related with the decrease of phytoplankton (Pigneur *et al.* 2014) can't be counterbalanced by other primary production like macrophytes due to important channelization and cleaning realised in the Meuse River during the last century. On the other hand, massive filtration of the water column and excretion of organic matter by

invasive molluscs must enhance the benthos and beneficiate to benthos organisms (Werner & Rothhaupt, 2007).

Diminution of phytoplankton biomass at the Lixhe pass less influence fish fauna than at Tailfer. The correlation is not significant (Fig. 9a). Furthermore, Lixhe pass is situated lower in the basin river and benthic species represented a large part of fish population (Fig. 10). Benthic fishes were already affected by the capture diminution so the rarefaction of trophic resources in the water column can't be the only explanation. The most credible hypothesis is the Great Cormorant predation which was significantly correlated with fish population at Lixhe (p = 0.0261). This avian predator could eat daily between 401 to 423 g of fish from various species and class size (Evrard & Tarbe 2002) and could massively impact fish fauna when its population is excessive. This species arrived at Lixhe in 1992, the mean individuals wintering along the reach during 1995 to 2000 was close to 972, with a max of 1370 individuals in 1997 (Paquet, 2011). The number of Great cormorant at Lixhe followed their prey population and decrease massively in the beginning of the 2007 to 2012 with a mean of individuals wintering closed to 342. Unfortunately, we don't have fish data anterior to the Great cormorant arrival. At Tailfer, the Great cormorant was present since 1994, with a pick of 928 individuals wintering in 2001 along the reach and must have influenced fish population too.

Fish population structures have undergone deep modifications between the last decades. Fish population was really balanced during the 1990s contrary to the beginning of the 2000s which saw their stability disappear as illustrated by figures 5b and 9b where recently groups are more scattered. Currently, fish populations of the River Meuse are disrupted due to environmental modifications caused by allochthonous species like invasive molluscs, Great cormorant, asp and wels catfish. We can suppose that fish populations cross a transitional period which must be stabilised when biocenose will find a new equilibrium. But transition period should not happen quickly because we have recently found in the lower Belgian Meuse a new allochthonous species, potentially invasive, the Western tubenose goby (*Proterorhinus semilunaris*) (Cammaerts *et al.*, 2012) which consumed molluscs and could reduce invasive bivalvia population.

Conclusion

The River Meuse is a eutrophic river that corroborates well with the high densities of roach found in the 1990s and beginning of the 2000s. Current estimates reveal low stocks in three reaches with less than 500 roach ha^{-1}. This sharp decline had little impact on growth and mortality. Analysis of fish pass reveals a deep change in fish structure. Since the mid-2000s, a drastic decline in phytoplankton biomass is highlighted and linked to invasion of Asian clams, *Corbicula*. Nutrients, except soluble reactive phosphate still sufficient for plankton growth, show no significant decrease (Pigneur *et al*. 2014). We suspect a "bottom-up" effect on fish populations following the 70% loss of primary production which cannot be replaced by macrophytes because of channelization. A "top-down" effect is also suggested as population of Great Cormorant decreases since 2003 along the River Meuse after a period of outbreak.

Ce qu’il faut retenir de ce chapitre

Dans ce second chapitre, nous évaluons l’évolution des populations de gardons en Meuse belge basée sur des données de capture-marquage-recapture, des inventaires au filet maillant et de monitoring de deux passes à poissons. Les 3 méthodes utilisées délivrent un message similaire, les populations de gardons ont décru de plus de 90% en l’espace d’une dizaine d’années en Meuse belge.

Les causes de cette diminution restent indeterminées mais l’analyse taxonomique et fonctionnelle laisse suggérer que la diminution des ressources planctoniques et l’augmentation des densités du grand cormoran peuvent avoir une influence sur les communautées. La diminution du phytoplancton et du zooplancton pourrait limiter le développement ou la survie des gardons lors des plus jeunes stades ontogéniques, et l’augmentation de la densité de prédateurs aviaires influencer la survie des gardons adultes.

Néanmoins, une étude des peuplements de poissons réalisée par Alonso *et al.* en 2014 révèle que la population de gardon est restée stable en Meuse française au cours de la même période en dépit des pressions similaires exercées sur les populations. Au cours des chapitres suivants, nous émettons l’hypothèse que les biefs aménagés pour la navigation fluviale offrent une plus faible hétérogénéité de l’habitat ainsi qu’une diversité de ressources basales moins importante que les biefs impropres à la batellerie. En cas de raréfaction des ressources planctoniques, ces facteurs pourraient impacter les populations ainsi que la niche trophique des communautés.

Chapitre 3

Impacts of reduced habitat diversity and impaired phytoplankton availability on the potential trophic niches of aquatic communities

Avant-propos

Le 3ème chapitre analyse les niches trophiques potentielles des communautés de macroinvertébrés et de poissons de deux stations de la Meuse différement aménagées par l'Homme. Avec une approche basée sur les traits d'histoire de vie, nous comparons l'effet de la diminution du phytoplancton au cours du temps sur les niches trophiques potentielles des communautés en fonction du degré d'aménagement de la Meuse. Nous émmettons l'hypothèse que les communautés de poissons et de macroinvertébrés de la Meuse française ont été moins perturbées par la diminution des ressources planctoniques qu'en Meuse belge du fait de la diversité des habitats et potentiellement des ressources alimentaires alternatives disponibles (périphyton, végétation aquatique, ripisylve…).

Ce chapitre est basé sur une compilation de données mises en forme, traitées et interprétées par l'auteur.

Impacts of reduced habitat diversity and impaired phytoplankton availability on the potential trophic niches of aquatic communities

Abstract

Large rivers are particularly disturbed by physical regulation affecting quality of habitat and reducing the diversity of trophic resource. In this study, we analyzed the long-term trophic niches trends of macroinvertebrate and fish communities from two differentially regulated reaches of the Meuse River, both affected by reduced water column resources. We used trait-based approaches to characterize the potential trophic niches of the communities. We hypothesized that the impact of the planktonic decrease should have been lower in the less regulated reach, regarding both community indices. We provided evidence that the potential trophic niches of the communities were affected at both sites by the phytoplankton decrease with a greater impact on the most altered site. In the less regulated reach, the functional equitability and the specialization had increased in the trophic niches of the macroinvertebrate communities during the decrease of the planktonic resources while the indices stayed constants in the channelized reach. The hydraulic perturbations of the Belgian part of the River Meuse appear to have homogenized the potential trophic niche of the communities which could hypothetically contributed to decrease the resilience of the ecosystem and tend to magnify trophic disturbances. However the results highlighted previously, based on the potential traits, have to be confirmed by the analysis of the realized trophic niche with another approach as stable isotopes.

Introduction

Large European rivers like Rhone, Danube, Rhine and Meuse are particularly affected by physical regulation mainly to control flood and facilitate fluvial navigation (Tockner *et al*., 2009). Dam constructions profoundly affect depth, current velocity and flow (Middelkoop *et al.*, 2001) and river channelization reduces exchange between the flood plain and the river bed. The combined influences of these pressures negatively affected freshwater fish and macroinvertebrate populations (Dudgeon *et al.*, 2006). In a retrospective analysis of American western basins for instance, Gido and colleagues (2010) found that more than 50% of species recorded in historic collections disappeared, as a result from changes in flow regime and land use, as well as from loss of habitat .

A well-established mechanism described by the stream ecologists is the role of habitat (see River Habitat Templet theory for more information; Townsend & Hildrew, 1994), in terms of heterogeneity (distribution), diversity (number of types), complexity (spatial arrangement) and variability over time (Ward & Stanford, 1995b). These habitat features play a key role in the preservation of biodiversity (Ligeiro *et al.*, 2013) and in the capacity of the communities to cope with environmental disturbances (Palmer *et al*., 2010). Many freshwater organisms need a large combination of habitats and resources to accomplish their life cycle and the rarefaction of spawning, feeding or refuge habitats has direct consequences on the diversity and abundance of the most sensitive species (Ward & Stanford, 1995a).

The structure and composition of the macroinvertebrate and fish assemblages are directly linked with habitat heterogeneity and resource availability which allow increasing trophic niche size and reducing intra- and interspecific niche competition (Zeni & Casatti, 2014; Faulks *et al.*, 2015). For example, measures for flood management affecting transversal connectivity, bank erosion and substrate sedimentation have contributed to reduced biological production of rivers and floodplains and to decreased diversity and quality of habitats (Aarts *et al*., 2004). Some authors have demonstrated that in unregulated South American rivers, the flood pulse period increased the resource use diversification of consumers and the productivity of macroinvertebrate and fish (Castello *et al.*, 2015; Sepúlveda-Lozada *et al.*, 2017). Poorly adapted species could decrease in favor of generalist species (Villéger *et al.*, 2010) which take advantage of vacant niches or predation facilitation on taxa destitute of adequate shelter (Hermoso *et al.*, 2011). Resource fluctuation in an ecosystem could be considered as perturbation which engender a shift in the trophic structure by remodeling interactions (Cucherousset & Olden, 2011). As examples, we can cite in European and American freshwaters and lakes the massive consumption of phytoplankton by the zebra mussel (*Dreissena polymorpha*) which had in few years created a cascading effect influencing many taxonomic groups from sediment bacteria (Frischer *et al*. 2000; Smith *et al*. 2011) to piscivorous fish (Daniels *et al*. 2005; Ward & Ricciardi 2007).

To highlight response of biocenosis following to abiotic and/or biotic disturbances and to understand food web functioning, many studies recommended the functional diversity approach at the community scale (Díaz & Cabido, 2001; Villéger *et al.*, 2008). Macroinvertebrates and fish are good indicators of environmental degradation (Marzin *et al*. 2012), hydromorphological stress (Poff & Zimmerman, 2010) and changes in nutrient and temperature patterns (Cross *et al.*, 2005; Gafner & Robinson, 2007). Furthermore, macroinvertebrate are particularly interesting to highlight trophic shift due to their diversified feeding well described by ecologists (Tachet *et al*., 2010) and their key position between primary producers and higher trophic levels (De Castro *et al.*, 2016).
The functional method was adapted from the concept of niche developed by Charles Elton. It attributes to each species a role in the ecosystem (Elton, 1927) which can be interpreted as a guild or a functional group in agreement to their trophic relationships (e.g. predator, filter-feeder…) (Devictor *et al.*, 2010). Connecting the position of each species or guilds together forms an ecological trophic network which represents the functional niche of the community, while studying the distribution and the evenness of these species or guilds in the community trophic niche allows to determine the type and the intensity of the disturbances (Devictor *et al*., 2010; Mouillot & Graham, 2013). In a degraded habitat or perturbed environment, mortality rates increase and trophic resources decrease (Mouillot *et al.*, 2013), which lead to (i) an increase of trophic niche overlap which tends toward a competitive exclusion (Jackson *et al*., 2001; Haddad *et al*., 2008), (ii) a reduction of the functional evenness due to exclusion of some trophic guilds or species (Mouillot *et al.*, 2013) and (iii) a decrease of specialist species more sensitive than generalists (Devictor *et al.*, 2010). For example, omnivorous fish suffered less from river regulation and habitat destruction than specialized fish which tend to rarefy in large rivers (Aarts *et al*., 2004).

The utilization of the potential feeding traits of communities allowed to quantitatively estimate trends in trophic structure of community niches (Blanck *et al.*, 2007; Tachet *et al.*, 2010; Cucherousset & Villéger, 2015). Each species trait values (*e.g*. scraper, invertebrate feeders…) weighted by their abundances are transformed as coordinates which define the trophic multidimensional space occupy by the community, i.e. the fundamental trophic niche (Villéger *et al.*, 2010). Some ecological indices (*e.g*. richness, evenness, divergence…) of functional diversity were established to analyze the trophic structure of the communities along a spatial and temporal gradient.

In this study, we used long-term trait-based analyze to characterize changes in the theoretical and observed trophic structures of macroinvertebrate and fish communities following a massive phytoplankton decrease (Latli *et al*., 2017) in two reaches of the Meuse River differently regulated.

We hypothesized that:

(i) phytoplankton reduction in the Meuse river has deeply affected trophic functioning by reducing the trophic functional diversity, evenness and specialization of

communities with a lesser effect in the more resilient habitat, the less channelized reach,

(ii) the potential trophic niche was larger in the less channelized reach due to the probable availability of more varied basal food sources (as periphyton, aquatic vegetation…).

Materials and Methods

Study area

The Meuse River rises on the Langres plateau in North-Eastern France, flows through Belgium and Netherlands, and ends up in the Dutch delta after joining the Lower Rhine. The total length of the river is close to 925 Km for a catchment area of 36,011 km². The main characteristics of the river basin and of the river itself were summarised in Descy *et al*. in Tockner *et al*. (2009). During the last 150 years, the river bed was heavily transformed for navigation and flood control mainly along the Belgian section. Sixteen dams are located along the Belgian sector and river channelization profoundly affects depth, current velocity and lateral connectivity. By contrast, the French section conserves their ecological functions and biodiversity due to relatively limited flow regulation measures (Grevilliot *et al*. in Tockner *et al*., 2009). The shallowness of the river allows the development of diverse vegetation from periphyton to helophytes and hydrophytes. The riparian zone is quite well developed and contributes to increase the habitat heterogeneity (Descy *et al*. in Tockner *et al*., 2009). During the last 25 years on the French and Belgian River Meuse, water temperature increased close to 1°C and the phytoplankton and zooplankton biomass decreased (- 85%) as well as orthophosphate, nitrate and suspended mater concentrations (Latli *et al*., 2017). The present study was conducted in three reaches of the River Meuse: Ham sur Meuse (N 50° 6’ 36”, E 4° 46’ 49”) in France, Waulsort (N 50° 12’ 56”, E 4° 49’ 37”) and Tailfer (N 50° 23’ 53”, E 4° 52’ 54”) in Belgium, located 469, 488 and 522 km respectively from the source.

Data acquisition

Macroinvertebrates

Data were provided from EDF for the French site and from DEMNA for the Belgium site. Benthic macroinvertebrates were sampled in summer from 1998 to 2010 at Ham sur Meuse (France) with the IBGN (“Indice Biologique Global Normalisé”; NF T90-350, 2009) protocol. In Waulsort (Belgium), a protocol adapted for deep rivers and derived from the IBGA (“Global Biological Index Adapted to large freshwater rivers”, Gay Environnement & Agence de l’Eau Rhône-Méditerranée-Corse, 1997) was used (Usseglio-Polatera & Beisel, 2002). Taxon abundances (x) were determined and identification levels were harmonised at the family level. Taxa abundances were log(x+1) transformed to normalize the distributions.

Fishes

Data were provided by EDF and ONEMA for the French site and by SPW-SP and Namur-University for the Belgium site. In France, electrofishing (from a boat) was used in spring, to

sample fish communities over the 1987-2011 period at Ham sur Meuse. In Belgium, data have been provided by the survey of fish passages in fish ladders at Tailfer over the 1989-2011 period. Fish were collected daily in a trap placed in the upper pool of the ladder when the migration peaks occurred, and twice a week outside the major migration period. All the fish species were identified and species abundances were estimated. Annual fish abundances were expressed as monthly averages. The whole data set was log(x+1) transformed to normalize abundance distributions.

Data analysis

Biological trait and functional metrics measurement

We focused on two congruent life-history traits selected from published European data bases, the trait feeding habits for the macroinvertebrates (Tachet *et al.*, 2010) and the trait feeding diet for fish (Blanck *et al*., 2007). Each trait was resolved in different categories (Figures 1 & 2). Each taxon was coded according to its affinity to each trait category using a fuzzy coding approach (Chevenet *et al.*, 1994). The resulting relative affinity scores of the taxa were multiplied by their ln(x+1)-transformed abundances at a given date (i.e. within a given invertebrate – or fish - assemblage sample). The weighted affinity scores of the categories of each trait were finally divided by their sum, providing the mean (relative) trait profile of the assemblage at a given date (see e.g. Archaimbault *et al*., 2009 for further detail).

Based on this matrix, we created a functional-trait space using a principal component analysis, as proposed by Villéger *et al*., (2008) in order to describe the functional characteristics of the communities with three different metrics (Villéger e*t al.*, 2008) :

- Functional richness (FRic): This metric considers the volume of the hull filled by the community in the functional-trait space. A large volume involves an important diversification of the functional characteristics of the community.
- Functional evenness (FEve): This metric relates the regularity with which the functional-trait space is filled by species weighted by their abundance. This index decreases when a significant number of individuals have the same functional characteristics.
- Functional specialisation (FSpe): This metric estimates the mean distance between species in the functional-trait space weighted by their abundance. As for the previous index, FSpe decreases when a significant number of taxa have the same functional characteristics.

All of these indexes tend to decrease with perturbations (Mouillot *et al.*, 2013).

Statistical analysis

Temporal trends of categories of trait and functional metrics were examined over the study period using Generalized Additive Models (GAM; Fewster *et al*., 2000) and modelled as a smooth nonlinear function of time. Autocorrelation error was reduced by adding a residual autocorrelation structure, optimized by minimizing the AIC criterion over several combinations of autoregressive parameters (Zuur *et al*., 2009). We statistically compared for

each categories of trait and functional metrics measured the site effect, the chlorophyll-a concentration effect and their interaction with a linear least-squares regression analysis. Normality of data and residuals were analysed with a Shapiro-Wilk test (Shapiro & Wilk, 1965).

Results

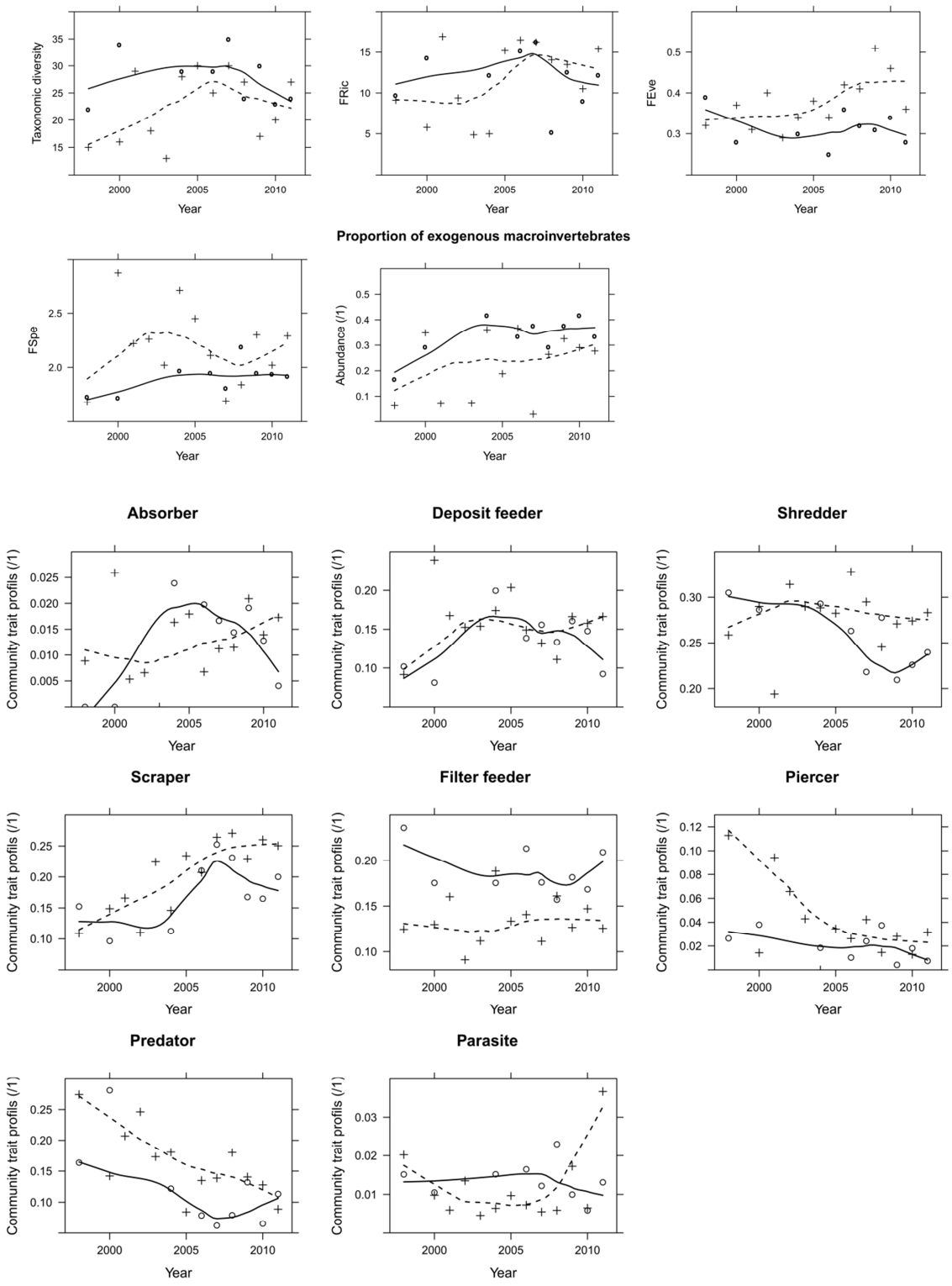
The taxonomic diversity and the portion of the functional space (FRic) filled by the macroinvertebrate communities of the two studied sites were relatively constant over time (Table 1). However, at Ham sur Meuse these indices slightly increased and became similar to those at Waulsort. The macroinvertebrate taxonomic diversity was higher at Waulsort than at Ham sur Meuse and did not change over time but inside the functional space, many changes occurred across time or sites. The relative abundance of the numerous traits (FEve), in other words the distribution of the potential resources used by the macroinvertebrate communities increased in Ham sur Meuse in relation with the chlorophyll-a concentration (pval = 0.04), but did not change significantly in Waulsort. The functional specialization (FSpe) increased in France but remained constant in Belgium (R^2 = 0.49, pval = 0.03 and 0.44 respectively).

Table 1: Statistical evaluation of time and site effects with a linear least-squares regression analysis of functional metrics and utilization frequency of eight categories of the trait feeding habits of the macroinvertebrate communities on two sites of the Meuse River (Ham sur Meuse in France and Waulsort in Belgium) during the 1998-2011 period and four categories of the trait feeding diets of the fish communities on two sites of the Meuse River (Ham sur Meuse in France and Tailfer in Belgium) during the 1989-2011 period.

				Temporal evolution			Linear regression			
		Index	R^2-adj (/1)	France		Belgium		P-val			R^2-adj (/1)
				Trend	p-val	Trend	p-val	Site	[Chla]	[Chla]*Site	
Functional metrics	Macroinvertebrate	Taxonomic diversity	0.01	-	0.23	-	0.89	**0.02**	0.11	0.08	0.19
		FRic	0.37	-	0.1	-	0.71	**0.01**	**<0.01**	**<0.01**	0.27
		FEve	0.14	↗	**0.04**	-	0.46	0.50	**0.03**	**0.04**	0.36
		FSpe	0.49	↗	**0.03**	-	0.44	0.06	0.42	0.25	0.15
	Fish	Taxonomic diversity	0.61	↗	**<0.01**	-	0.06	0.52	**0.02**	**0.03**	0.13
		FRic	0.51		0.1	↘	**<0.01**	**<0.01**	0.35	0.53	0.36
		FEve	0.72	↘	**<0.01**	↗	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.42
		FSpe	0.31	-	0.06	↘	**0.04**	**0.01**	0.46	0.59	0.15
Feeding habits	Macroinvertebrate	Absorber	0.32	-	0.43	-	0.06	0.99	0.22	0.83	0.2
		Deposit feeder	0.8	↗	**0.02**	↗	**0.02**	0.11	0.75	0.32	0.13
		Shredder	0.21	-	0.72	↘	**<0.01**	0.78	0.82	0.82	0.21
		Scraper	0.51	↗	**<0.01**	-	0.2	0.07	**<0.01**	**0.01**	0.53
		Filter-feeder	0	-	0.65	-	0.73	**0.05**	0.97	0.85	0.47
		Piercer	0.4	↘	**<0.01**	-	0.26	0.10	0.14	0.24	0.11
		Predator	0.58	↘	**<0.01**	↘	**<0.01**	0.08	**<0.01**	0.22	0.67
		Parasite	0.42	↗	**<0.01**	-	0.81	0.23	0.19	0.27	0
	Fish	Invertebrate feeders	0.86	↗	**<0.01**	↗	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.75
		Omnivorous	0.55	-	0.53	↘	**<0.01**	**<0.01**	0.15	0.06	0.46
		Piscivorous	0.26	↘	**<0.01**	-	0.66	**0.04**	0.13	0.36	0.11
		Carnivorous	0.92	↘	**<0.01**	↘	**<0.01**	**<0.01**	**<0.01**	0.21	0.66

Five macroinvertebrate traits significantly changed across time along the studied period (Table 1 and Figure 1). Abundance of predators significantly decreased over time at both sites ($R^2 = 0.58$) in relation with the chlorophyll-a concentration (pval < 0.01) and the proportion of piercers declined at Ham sur Meuse ($R^2 = 0.4$, pval < 0.01). Abundance of scrapers increased more at Ham sur Meuse ($R^2 = 0.51$, pval < 0.01) than at Waulsort, in relation with the diminution of concentration of chlorophyll-a (pval = 0.01). Whereas the amount of shredders declined at Waulsort ($R^2 = 0.21$, pval < 0.01), filter-feeders were significantly more abundant at Waulsort than at Ham sur Meuse ($R^2 = 0.47$, pval = 0.05).

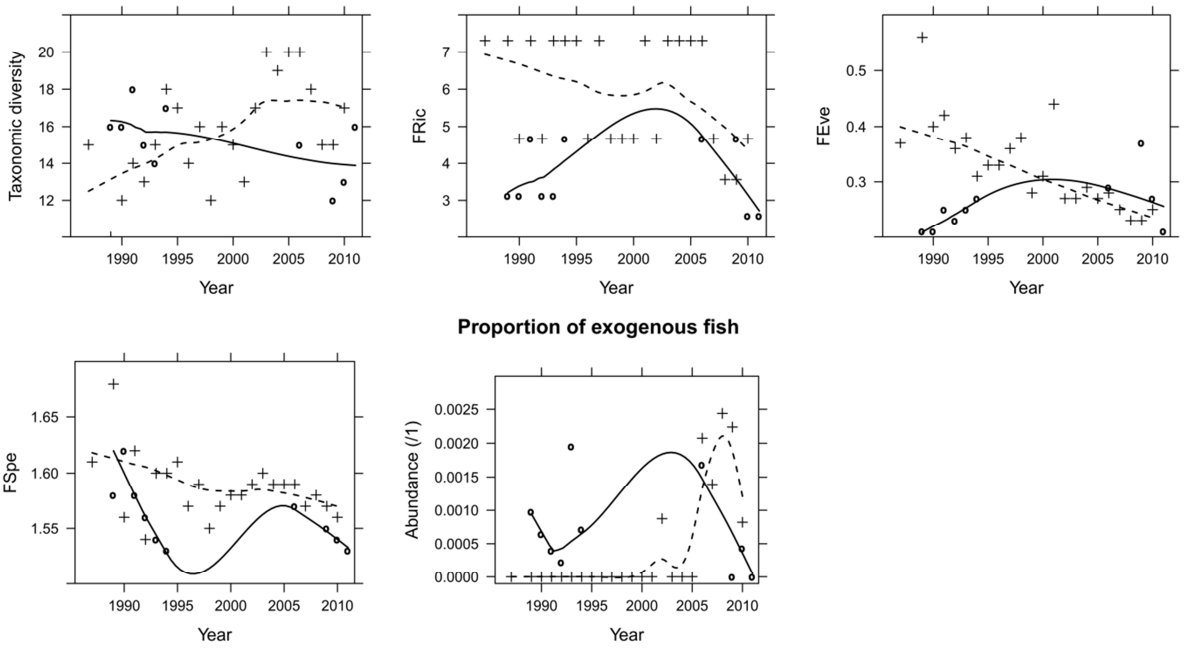
Figure 1: Temporal evolution of functional metrics and utilization frequency of eight categories of the trait feeding habits of the macroinvertebrate communities on two sites of the Meuse River during the 1998-2011 period. Temporal trends were modelled using a Generalized Additive Models with residual autocorrelation structure. Dashed line and “plus” corresponds to Ham sur Meuse site (France) and solid line and “circle” to Waulsort site (Belgium).

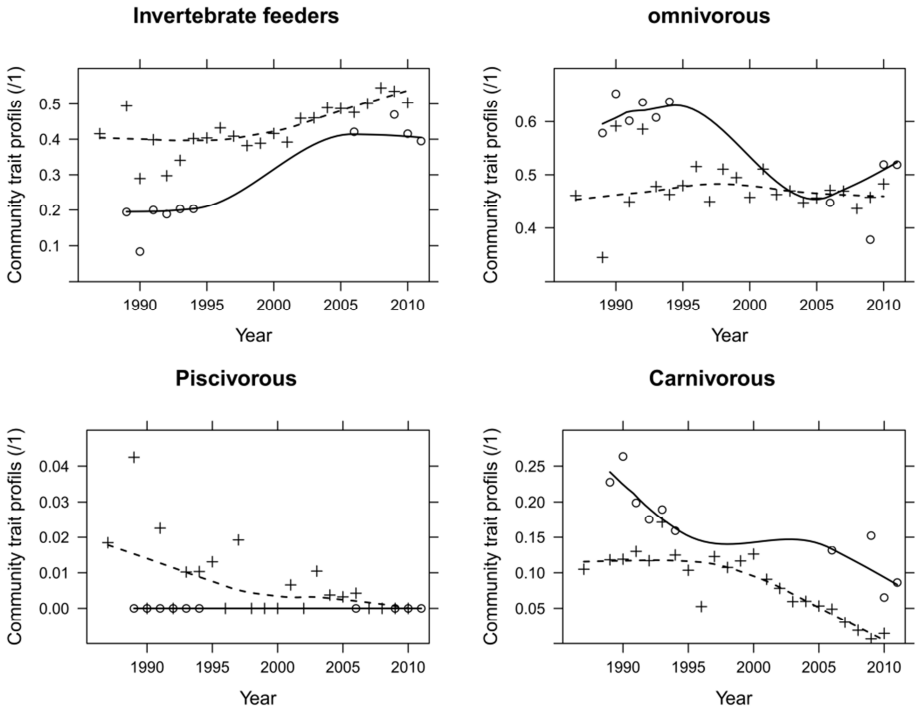


At Ham sur Meuse (Table 1, Figure 2), the taxonomic diversity increased over time (R^2 = 0.61, pval < 0.01) and slightly decreased in Tailfer (pval = 0.06) in relation with the chlorophyll-a diminution (pval = 0.03). Furthermore at Tailfer, the trophic niche (FRic) decreased (R^2 = 0.51; pval < 0.01) as well as the relative abundance of the specialized traits (FSpe) used by the fish community (R^2 = 0.31; pval = 0.04) which stayed globally lower in Belgium (respectively pval <0.01 and pval = 0.01) than in France. However, in Ham sur Meuse FEve strongly decreased over time (R^2 = 0.72, pval < 0.01) in relation with chlorophyll-a concentration (R^2 = 0.42, pval < 0.01), while it increased in Tailfer (pval < 0.01).

All of the trophic traits studied significantly changed across time and sites along the studied period (Table 1 and Figure 2). Abundance of invertebrate feeders increased strongly (R^2 = 0.86, pval < 0.01) at both sites in relation with the chlorophyll-a concentration, but the augmentation was higher in Belgium than in France. However, omnivorous taxa were less represented at Tailfer and stayed constant at Ham sur Meuse (R^2 = 0.55, pval < 0.01 and pval = 0.53 respectively). Abundance of predators, carnivorous and piscivorous fish, significantly decreased at Ham sur Meuse (respectively R^2 = 0.92, pval < 0.01 and R^2 = 0.26, pval < 0.01). At Tailfer, the abundance of carnivores also decreased over the studied period (pval < 0.01) but they were less represented in Belgium than in France (R^2 = 0.66, pval < 0.01). No piscivorous species were caught in Tailfer.

Figure 2: Temporal evolution of functional metrics and utilization frequency of four categories of the trait feeding diets of the fish communities on two sites of the Meuse River during the 1989-2011 period. Temporal trends were modelled using a Generalized Additive Models with residual autocorrelation structure. Dashed line and “plus” corresponds to Ham sur Meuse site (France) and solid line and “circle” to Tailfer site (Belgium).





Discussion

Our study provides evidence that the dramatic decrease in phytoplankton which occurred in the 2000s in the Meuse River (Latli *et al*., 2017) has clearly affected the potential trophic niche of the macroinvertebrate and fish communities of both studied sites. One key result is that deposit feeders have benefited from the increase in benthic resources (Table 2) following the massive consumption of phytoplankton by invasive mollusks, which have contributed to transfer organic matter from the water column to the benthos (Pigneur *et al.*, 2014). In parallel, the proportion of invertebrate feeders in the fish communities has increased (Table 2), possibly as a result of an increase of macroinvertebrate density. By contrast, the proportion of predators has declined (Table 2) in both communities but this trend may have been more the consequence of an increased top-down pressure (i.e. predation by the invasive Great cormorant) than to a bottom-up effect related to the decrease of water column resources (Latli *et al*., 2017).

Another result from this study is that the communities of the most regulated site have been more affected by the phytoplankton decrease. Particularly, there was a strong association between the shift of trophic niche in the macroinvertebrate community and the habitat quality. The potential trophic niche was smaller in the Belgium site than in the more natural French site, with fewer specialist taxa (Table 1) which implies a stronger trophic competition in case of resource diminution. In the French site, the macroinvertebrate could benefit from an additional resource, the periphyton whose development was limited in Belgium due to the channelization of the river. The number of scrapers (mainly molluscs) strongly increased in France in relation with the decrease of the phytoplankton, which resulted in an improvement of water transparency, promoting periphyton and macrophyte growth in the shallowest parts of the river. Furthermore, shredder abundance (*i.e.* trichoptera) declined in the Belgian site

while it remained unchanged in France, possibly as a result of stronger trophic competition in Belgium following to a lower diversity of resources. Moreover, at Waulsort, the number of invasive macroinvertebrates in the community was higher than that at Ham sur Meuse, which can exacerbate the trophic competition. Sax and colleagues (2007) observed that a less diversified system, with homogeneous functions in the community, facilitated emergence of exogenous species which can created an imbalance in the system and/or increases competition.

Fish trophic guilds were also impacted by the resource decrease, mainly in the more regulated site where the omnivorous fish were affected by the severe decrease in zooplankton density (Pigneur *et al*., 2014). Between the period 2010-2012 and the 1990's, zooplankton abundance decreased dramatically, and the present biomass is nowadays less than 2% of what it used to be (unpublished personal data). The biomass of Roach (*Rutilus rutilus*), which dominated the community in the Belgian part of the Meuse River during the 90's, has been reduced by 85%, mainly as a result of the collapse of the water column resources (Otjacques *et al*., 2015; Otjacques *et al*., 2016). However, this impact was lower in the less regulated part of the Meuse River in France (Alonso *et al*., 2013). In parallel, the roach decline could have allowed the increase of the trophic evenness of the fish community in Belgium until the 2000's (Table 1).

The hydraulic perturbations of the Belgian part of the River Meuse appear to have homogenized the potential trophic niche of the communities (Table 1). However, a high variability of functional groups in a community contributes to increase the resilience of the ecosystem and tend to absorb disturbance by retaining the same structure or function in the system (Elmqvist *et al.*, 2003). When the resilience of an ecosystem declines, a small incident can cause a shift in the community (Folke *et al*., 2004), as we observed in the more regulated river section, where the trophic resource diminution induced a shift from water column feeders to benthic feeders. Eventually, the shift could be irreversible, or really hard to inverse, and the return to the previous situation would require a substantial modification of the biotope (e.g. hydrological, climatic, trophic…; Folke *et al*., 2004). Moreover, as in the case of most disturbed ecosystems, the system did not return to the original situation because the deviations from environmental conditions had affected ecosystem dynamics and profoundly altered the structure and the functioning of the communities (Duarte *et al*., 2009). Cross and colleagues (2013) observed on the regulated part of the Colorado River communities with low species diversity, extremely sensitive to invasion, which exhibited changeable structural and functional properties (Cross *et al*., 2011).

Conclusions and caveats

Functional traits have been considered as effective predictors of ecosystem processes, allowing to reveal disturbances in community structure from environmental alterations (Mouillot *et al.*, 2013). In this study, the functional indices based on the long term evolution of the potential trophic niche showed that (i) the decrease of phytoplankton had affected the

potential trophic niche of the macroinvertebrate and fish communities in both sites with a greater impact on the most altered site, (ii) fish communities had also been disturbed by the phytoplankton decrease which had benefited to benthic invertebrate-feeders at the expense of water column omnivorous fishes, (iii) the equitability and the specialization had increased in the trophic niches of the macroinvertebrate communities. However, the results highlighted previously based on the potential traits, have to be confirmed by the study of the realized trophic niche with another approach as stable isotopes.

Ce qu'il faut retenir de ce chapitre

Dans le 3ème chapitre, nous avons émis l'hypothèse que les communautés de poissons et de macroinvertébrés de la Meuse française ont été moins perturbées par la diminution des ressources planctoniques qu'en Meuse belge du fait de la diversité des habitats et potentiellement des ressources alimentaires alternatives disponibles (périphyton, végétation aquatique, ripisylve…).

Nous avons démontré que la réduction du phytoplancton a affecté les niches trophiques potentielles des communautés des deux stations. Toutefois, au fur et à mesure de la diminution du phytoplancton, la spécialisation alimentaire ainsi que la diversité des ressources potentiellement utilisées par la communauté tendent à augmenter en France tandis qu'elles restent stables en Belgique. Ce résultat suggère que l'homogénéisation de l'habitat peut réduire sa résilience lors de perturbations trophiques.

Dans le chapitre suivant basé sur des données isotopiques nous étudions l'origine des matières carbonées assimilées par la communauté de macroinvertébrés en comparant deux biefs de la Meuse différemment aménagés. Nous analysons également la compétition trophique entre différents taxons aux régimes alimentaires potentiels proches. Nous émettons l'hypothèse que le recouvrement des niches trophiques est plus important en Meuse Belge du fait d'une plus faible diversité potentielle des ressources primaires.

Chapitre 4

Overview of trophic niche and food competition of macroinvertebrate and fish assemblages in two reaches differently regulated of a large-river in a low phytoplankton context

Avant-propos

Au cours de ce 4ème chapitre nous cherchons à caractériser les niches trophiques réalisées des assemblages de macroinvertébrés et de poissons de deux stations de la Meuse différement aménagées par l'Homme. Basée sur une analyse des isotopes stables, nous modélisons dans un premier temps les ressources primaires utilisées par la communauté de macroinvertébrés sur les deux sites. Dans un second temps nous comparons la compétition alimentaire, via une analyse de recouvrement des niches isotopiques, entre les populations de différents taxons ayant un régime alimentaire théorique similaire.

L'inventaire ainsi que la préparation des échantillons ont été menés par l'auteur et "son" équipe. L'analyse élémentaire des échantillons a été réalisée à l'Université de Liège (laboratoire d'océanologie) par l'équipe de Lepoint G. Les chapitres 3 et 4 ont été soumis en une unique publication dans le journal hydrobiologia par le doctorant.

Latli A, Michel LN, Mathieu F, Jonathan M, Lepoint G, Patrick K (2018) Impacts of reduced habitat diversity and impaired phytoplankton availability on large-river food web functioning.

Overview of trophic niche and food competition of macroinvertebrate and fish assemblages in two reaches differently regulated of a large-river in a low phytoplankton context

Abstract

Large rivers are particularly disturbed by physical regulation affecting quality of habitat and reducing the diversity of trophic resource. In this study based on stable isotope approaches, we characterized the realized trophic niches of macroinvertebrate and fish communities and the competition among taxa from two differentially regulated reaches of the Meuse River, both affected by reduced water column resources. We hypothesized that the trophic niche of communities was wider and the niche overlap was smaller in the less regulated reach due to a potential higher availability of diversified basal resources. We provided evidence that (i) the trophic niche was slightly smaller in the channelized sector, with a significant contribution of allochthonous detritus and bryophytes at both sites (ii) taxa in the most disturbed site had a lower trophic niche overlap between sympatric consumers.

Introduction

Diversity of microhabitats and presence of riparian areas directly influence abundance and quality of available food sources of the whole riverine ecosystem (Pusey & Arthington, 2003). Autochthonous production (periphyton, aquatic macrophytes…) depend mainly on the type of substrate and on river depth (Vadeboncoeur & Lodge, 2000) and allochthonous resources are correlated with riparian canopy width (Pusey & Arthington, 2003; Ferreira *et al.*, 2012). The structure and composition of the macroinvertebrate and fish assemblages are directly linked with habitat heterogeneity and resource availability which allow increasing trophic niche size and reducing intra- and interspecific niche competition (Zeni & Casatti, 2014; Faulks *et al.*, 2015). For example, measures for flood management affecting transversal connectivity, bank erosion and substrate sedimentation have contributed to reduced biological production of rivers and floodplains and to decreased diversity and quality of habitats (Aarts *et al*., 2004). Some authors have demonstrated that in unregulated South American rivers, the flood pulse period increased the resource use diversification of consumers and the productivity of macroinvertebrate and fish (Castello *et al.*, 2015; Sepúlveda-Lozada *et al.*, 2017).

A diversified habitat offers many resources in terms of quality and availability (Jackson *et al*., 2001) but also many shelters allowing organisms to resist disturbances and recolonize the environment. Habitat alterations weakens the system and makes it more sensitive to stochastic events (Scheffer *et al*., 2001) which could induce an abrupt shift in the communities. Poorly adapted species could decrease in favor of generalist species (Villéger *et al.*, 2010) which take advantage of vacant niches or predation facilitation on taxa destitute of adequate shelter (Hermoso *et al.,* 2011). Resource fluctuation in an ecosystem could be considered as perturbation which engender a shift in the trophic structure by remodeling interactions (Cucherousset & Olden, 2011). As examples, we can cite in European and American freshwaters and lakes the massive consumption of phytoplankton by the zebra mussel (*Dreissena polymorpha*) which had in few years created a cascading effect influencing many taxonomic groups from sediment bacteria (Frischer *et al*. 2000; Smith *et al*. 2011) to piscivorous fish (Daniels *et al*. 2005; Ward & Ricciardi 2007).

To highlight response of biocenosis following to abiotic and/or biotic disturbances and to understand food web functioning, many studies recommended the stable isotope tools (Phillips *et al.*, 2005; Calizza *et al.*, 2012). Macroinvertebrates and fish are good indicators of environmental degradation (Marzin *et al*. 2012), hydromorphological stress (Poff & Zimmerman, 2010) and changes in nutrient and temperature patterns (Cross *et al*., 2005; Gafner & Robinson, 2007). Furthermore, macroinvertebrate are particularly interesting to highlight trophic shift due to their diversified feeding well described by ecologists (Tachet *et al*., 2010) and their key position between primary producers and higher trophic levels (De Castro *et al.*, 2016).

Analysis of stable isotopes, $\delta^{13}C$ and $\delta^{15}N$, were made in this study to quantitatively estimate trends in trophic structure of community niches (Cucherousset & Villéger, 2015). This approach is a common integrative tool used in trophic ecology to assess the realized ecological niche (Parnell *et al*., 2010), to measure the trophic relationship between preys and predators (Layman *et al*., 2012) and to quantify the trophic repercussions of many ecological processes (Fry, 2006). Moreover, this technic allows distinguishing the fluxes of energy between biotopes (*e.g.* terrestrial to freshwater ecosystems) (Fry, 2006).

In this study with a stable isotope approach, we characterized the observed trophic structures of macroinvertebrate and fish communities in a massive phytoplankton decrease context (Latli *et al*., 2017) in two reaches of the Meuse River differently regulated.

We hypothesized that:

(i) the trophic niche was larger in the less channelized reach due to availability of more varied basal food sources (as periphyton, aquatic vegetation…),

(ii) the niche overlap between taxa was weaker in the less channelized reach which allowed to reduce the trophic competition.

Materials and Methods

Study area

The Meuse River rises on the Langres plateau in North-Eastern France, flows through Belgium and Netherlands, and ends up in the Dutch delta after joining the Lower Rhine. The total length of the river is close to 925 Km for a catchment area of 36,011 km². The main characteristics of the river basin and of the river itself were summarised in Descy *et al*. in Tockner *et al*. (2009). During the last 150 years, the river bed was heavily transformed for navigation and flood control mainly along the Belgian section. Sixteen dams are located along the Belgian sector and river channelization profoundly affects depth, current velocity and lateral connectivity. By contrast, the French section conserves their ecological functions and biodiversity due to relatively limited flow regulation measures (Grevilliot *et al*. in Tockner *et al*., 2009). The shallowness of the river allows the development of diverse vegetation from periphyton to helophytes and hydrophytes. The riparian zone is quite well developed and contributes to increase the habitat heterogeneity (Descy *et al*. in Tockner *et al*., 2009). During the last 25 years on the French and Belgian River Meuse, water temperature increased close to 1°C and the phytoplankton and zooplankton biomass decreased (- 85%) as well as orthophosphate, nitrate and suspended mater concentrations (Latli *et al*., 2017). The present study was conducted in three reaches of the River Meuse: Ham sur Meuse (N 50° 6’ 36”, E 4° 46’ 49”) in France, Waulsort (N 50° 12’ 56”, E 4° 49’ 37”) and Tailfer (N 50° 23’ 53”, E 4° 52’ 54”) in Belgium, located 469, 488 and 522 km respectively from the source.

Stable isotope ratios

Sampling and isotope measurement

10 potential food sources (N = 507), 21 macroinvertebrate taxa (N = 418) and two fish species (N = 224) were sampled at both sites every two weeks during 2013 to 2015 summers (Table 1). As potential food sources we sampled various taxa of algae, bryophytes, hydrophytes, bottom-deposited organic matter, periphyton, suspended matter (from 0.6 to 30 µm and 30 to 100 µm) and bank vegetation. Macroinvertebrates were sampled with a Surber sampler (mesh size 500 µm) along the banks and by scuba diving in the channel. Macroinvertebrates were conserved 24h alive in water for gut clearance and then they were identified to the family level and frozen. We focused this study on 2 species of fish, the European chub (*Squalius cephalus*) and the Roach (*Rutilus rutilus*). Fish were sampled using an electrofishing approach from a boat along the banks, with a 7KW generator delivering a continuous current (150 - 300V at 3A). After sampling, fishes were identified, individually measured (total length) to the nearest mm with a measuring board, anesthetized, sacrificed using an excess of 2-phenoxyethanol (3mL/10L freshwater) and rinsed with deionized water. Finally, we sampled a part of the muscle of the fish before freezing.

Table 1: Sample numbers for stable isotope analysis

		Ham sur Meuse	Waulsort
Potential food sources	Algae	12	13
	Bryophyte	5	2
	Hydrophyte	9	7
	Decomposed organic matter	17	13
	Periphyton	32	28
	Fine suspended matter (0.6-30µm)	32	82
	Coarse suspended matter (30-100µm)	25	14
	Bank vegetation	11	25
	Small size macroinvertebrates	39	48
	Large size macroinvertebrates	56	37
Fish	*Squalius cephalus*	67	7
	Rutilus rutilus	63	87

		Ham sur Meuse	Waulsort
Macroinvertebrates	Ancylidae	1	1
	Baetidae	4	3
	Caenidae	3	2
	Chironomidae	7	23
	Corbiculidae	34	51
	Corophiidae	28	28
	Dreissenidae	0	20
	Ephemerellidae	2	4
	Ephemeridae	29	20
	Erpobdellidae	13	1
	Gammaridae	40	44
	Heptageneiidae	1	0
	Hydropsychidae	7	0
	Limnephilidae	6	4
	Lymnaeidae	3	3
	Mysidae	0	8
	Oligochaeta	8	11
	Physidae	2	0
	Rhyacophilidae	1	1
	Sialidae	1	1
	Simuliidae	3	0

Samples were individually treated. They were dried at 60°C for at least 48h and ground into a homogenous fine powder using a mortar and a pestle. Stable isotope ratios measurements were performed via continuous flow - elemental analysis - isotope ratio mass spectrometry at University of Liège, using a vario MICRO cube elemental analyser (Elementar Analysensysteme GmBH, Hanau, Germany) coupled to an IsoPrime100 mass spectrometer (Isoprime, Cheadle, United Kingdom). Isotopic ratios were expressed using the widespread δ notation (Coplen, 2011). Sucrose (IAEA-C6, $\delta^{13}C$ = -10.8 ± 0.5‰, mean ± SD) and ammonium sulphate (IAEA-N2, $\delta^{15}N$ = 20.3 ± 0.2‰, mean ± SD) were used as certified reference materials. Both of these reference materials are calibrated against the international isotopic references, i.e. Vienna Pee Dee Belemnite (VPBD) for carbon and Atmospheric Air for nitrogen. Standard deviations on multi-batch replicate measurements of lab standards (fish tissues) analyzed interspersed among the samples (2 lab standards for 15 samples) were 0.1 ‰ for $\delta^{13}C$ and $\delta^{15}N$. Glycine (Merck) was use as elemental standard, and elemental contents were expressed as percentage of dry mass.

Isotope data processing

Isotope metrics

Based on isotopic analysis we evaluated with the Layman *et al*. (2007) approach the trophic competition between macroinvertebrates or fish taxa with potential similar diet. This method estimates the trophic niche of a taxon by the area of a convex hull comprising all individual of a $\delta^{13}C$ and $\delta^{15}N$ isotope bi-plot. For reducing the sample size effect which could underestimate trophic niche area of small sample size, we calculated the SEAc metric (standard ellipse area corrected for small samples). This index encloses 40% of the isotope value of the population and represents the core isotopic niche of the studied taxa (Jackson *et al*., 2011). It illustrates the potential trophic competition among taxa according to the degree of human perturbation of the French and Belgian sites and to the resources availability.

We used a Bayesian mixing model (MixSIAR) to compare the diet composition of the macroinvertebrate community in each site (Parnell *et al.*, 2013). Trophic enrichment factors were determined for each resources using the formula proposed by Caut and colleagues (2009).

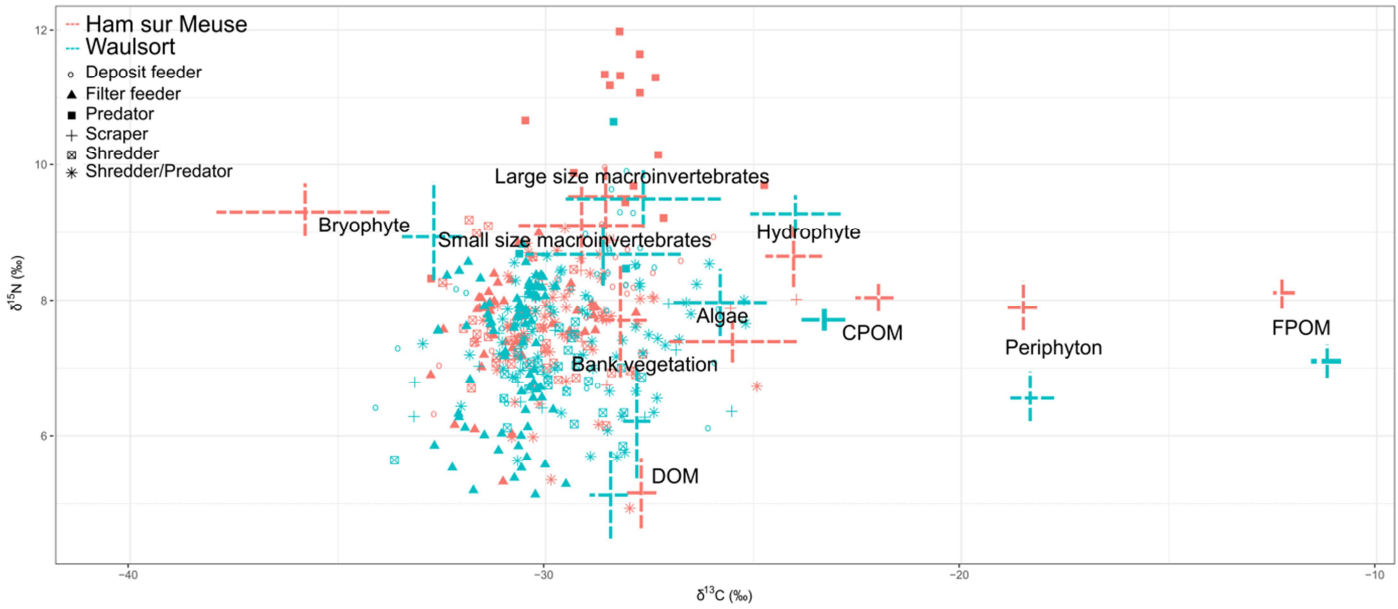
Analyses were carried out with the R-software (R 3.4 version, R Development Core Team, 2015) using various functions implanted in R by Villéger *et al*., (2008) for determining functional diversity metrics and the packages “MixSIAR” (Stock & Semmens, 2013) and “SIBER” (Jackson *et al*., 2011) for modelling the isotopic trophic niches.

Results

The stable C and N isotopic composition of the main sources of organic matter potentially edible by the macroinvertebrate communities of the two studied sites exhibited a strong similarity (Figure 1). Fine particulate matter (FPOM; 0.6 - 30 µm) and periphyton were much

less depleted in ^{13}C than the macroinvertebrate communities with a difference up to -8 and -9 % of $\delta^{13}C$ respectively at Ham sur Meuse and Waulsort, showing that these food items barely contributed to the diet of macroinvertebrates. By contrast the isotope signature of hydrophytes, algae and coarse suspended matter (CPOM; 30 - 100 µm) were closer to that the macroinvertebrate communities, indicating a greater contribution to macroinvertebrate diet. The main food source which was at the basis of the trophic network of the macroinvertebrate communities of the French and Belgian sites were the bryophytes (0.3 and 0.37 / 1 respectively) and the detrital organic matter (DOM; 0.26 and 0.29 / 1). The origin of these detritus was likely the bank vegetation, as indicated by the alignment between $\delta^{13}C$ mean values of the two sources. Although the ^{13}C positions of the two allochthonous resources were more or less in the midst of the macroinvertebrate communities, autochthonous matter appeared to contribute for just over half of the basal resources used by the macroinvertebrate community of both sites (0.52 / 1) with a dominance of the bryophytes.

Figure 1: $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values of the macroinvertebrate community sampled in the Meuse River at Waulsort (blue) and Ham sur Meuse (red) between 2013 and 2015. Symbols represent individual isotopic value of each macroinvertebrate captured, grouped by feeding groups (Tachet *et al.*, 2010). Mean values and standard deviations of potential food sources are represented by colored dashed lines (DOM: detrital organic matter, FPOM: fine particulate matter, CPOM: coarse suspended matter).



Although the communities of the two sites studied consumed in the same order of magnitude the same food sources (Figure 2), the communities shared only 65% of their isotope space (Figure 3). At Waulsort the community had a larger $\delta^{15}N$ gradient but a smaller $\delta^{13}C$ gradient than at Ham sur Meuse. The isotopic values of the macroinvertebrate community at Waulsort were more ^{13}C-depleted than at Ham sur Meuse while only one potential food sources sampled had more negative $^{13}C/^{12}C$ ratio (bryophyte). The main components involved were mostly Chironomidae, Trichoptera and to a lesser extent Corbiculidae (Figure 1).

Figure 2: Diet estimation of the macroinvertebrate communities based on the individuals $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values and the potential food sources sampled at Waulsort and Ham sur Meuse between 2013 and 2015 (see Figure 1).

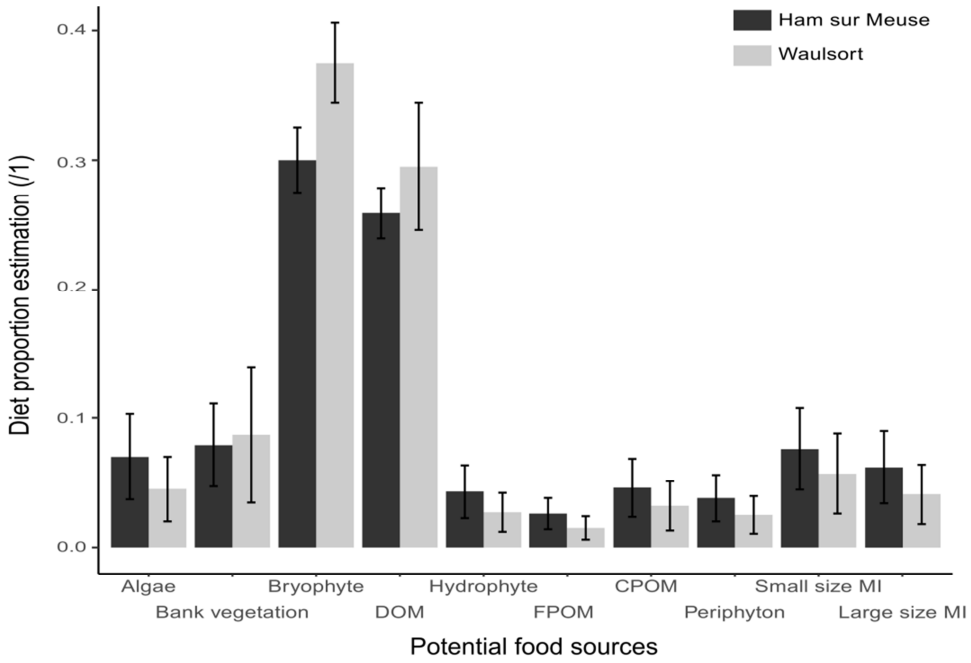
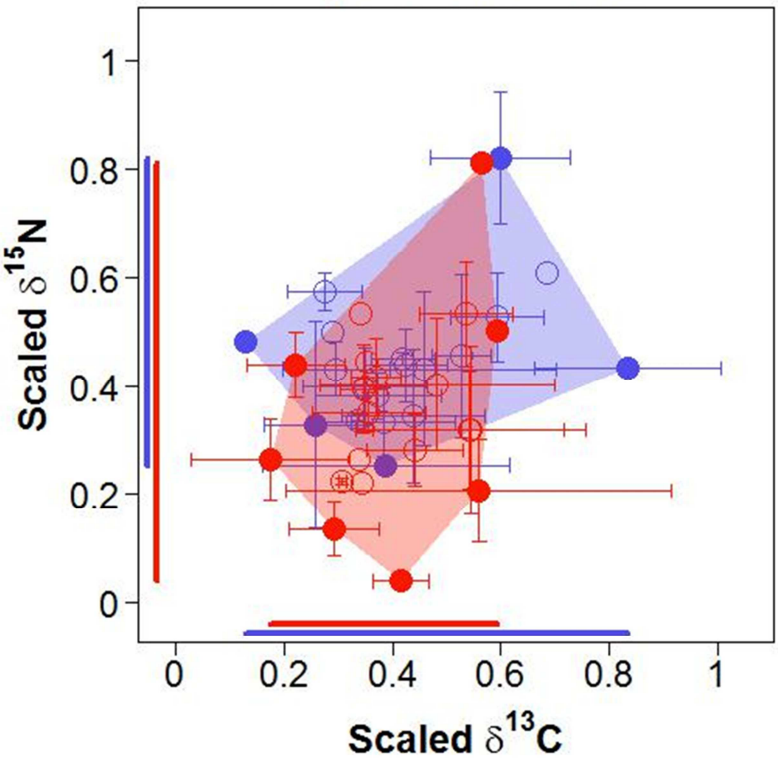


Figure 3: Isotopic overlap between two macroinvertebrate communities of the Meuse River from 2013 to 2015 in a two-dimensional isotopic space scaled by site. Blue and red correspond to isotopic space of, respectively, Ham sur Meuse (France) and Waulsort site (Belgium).Mean isotopic value (dot) and standard error (line) of each taxa is represented.



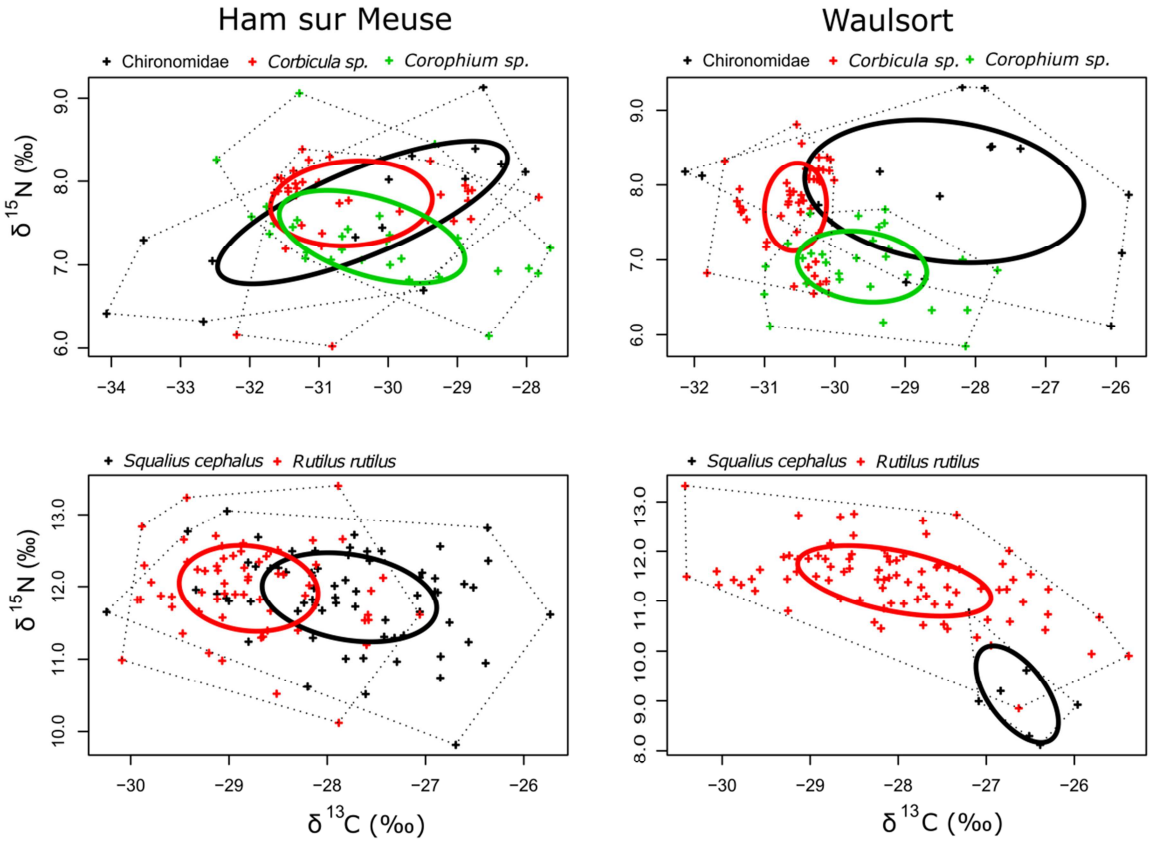
The two graphs on each row of figure 4 describe the isotope niche of taxa which were potentially in competition for a part of their diet. On the first row, 3 taxa were represented, the Chironomidae, an omnivorous family with multiple feeding habits (deposit feeder, filter feeder, shredder and predator; Tachet *et al*., 2010). The two other taxa (*Corbicula* sp. and *Corophium* sp.) are invasive in the Meuse River. *Corophium* sp. is a shredder / deposit feeder and *Corbicula* sp. is essentially filter-feeder, although the clam can switch to pedal feeding in the sediment when phytoplankton concentration is low (Werner & Rothhaupt, 2007). At both sites, the Chironomidae had a larger trophic niche (SEAc = 3.7 and 5.9 on Ham sur Meuse and Waulsort) than the two other taxa (SEAc < 2) and the niche overlap at Waulsort was close to zero, whereas it was around 0.2 at Ham sur Meuse (Table 2).

Table 2: Comparison of stable isotope overlap of the corrected standard ellipse area index for 5 macroinvertebrate taxa and 2 fish taxa sampled at two sites in the Meuse River between 2013 and 2015

	Ham sur Meuse	Waulsort	Overlap probability (/1): Ham sur Meuse > Waulsort
Chironomidae – *Corbicula sp.*	0.23	0.02	1
Chironomidae – *Corophium sp.*	0.19	0.02	0.97
Corbicula sp. – *Corophium sp.*	0.21	0.004	1
Squalius cephalus – Rutilus rutilus	0.11	0	1

On the last row of figure 4, the trophic niches of two omnivorous cyprinids are displayed. As previously, niche overlap was more pronounced at Ham sur Meuse (Table 2) and roach was more $\delta^{13}C$-depleted than chub (Figure 4).

Figure 4: Representation of the isotopic niches, from $\delta^{13}C$ and $\delta^{15}N$ values, for Chironomidae, *Corbicula* sp., *Corophium* sp., *Squalius cephalus* and *Rutilus rutilus* collected on the Ham sur Meuse and Waulsort sites of the Meuse River between 2013 and 2015. The corrected standard ellipse area (SEA_C) comprises 40% of the sample of each taxon (solid lines). The convex hull area (dotted lines) corresponds to the area encompassing all the mean location of the individuals of each taxa.



Discussion

Our study provides highlighted that macroinvertebrate communities consumed mainly two types of resources, the bryophytes and the detrital organic matter derived mainly from the bank vegetation. In both sites, the other sources of carbon as periphyton or suspended organic matter were positioned far away of the macroinvertebrate trophic niches. These results do not fit with the Riverine Continuum Concept (RCC; Vannote *et al.*, 1980), which considers that the primary food sources should be benthic autotrophs in shallow rivers (as the Ham sur Meuse site), whereas it should be fine particulate matter from upstream and/or the floodplain in a deep river (as the Waulsort site). However, our results agree with other concepts (Thorp *et al.*, 2006), which state that the main source of food in large river food origin may be derived from autochthonous production. Similarly, the flood pulse concept (Junk *et al.*, 1989) highlights the predominance of the terrestrial detritus, of vegetation from floodplain and of aquatic macrophytes as primary energy source. From stable isotope analysis, other studies provided evidence that algae and terrestrial organic matter decomposed by the microbial loop were the main carbon source used by metazoans (Lewis *et al.*, 2001; Delong & Thorp, 2006).

These studies highlight the key role of allo-and autochthonous detritus in the river food web of tropical and temperate large rivers (Thorp *et al.*, 2006) which have a large proportion of depositional habitats, particularly in sections located directly above large dams or in segments with alternating “fast” and “slow” current (Zeug & Winemiller, 2008).

In this study, in agreement with the literature, the range of $\delta^{13}C$ of the macroinvertebrate community was wider in the shallower, less regulated site of the river Meuse (Figure 3), with the accessory carbon sources slightly more consumed. This implies a greater diversity of potential basal sources at the base of the food web (Newton, 2010). The range of primary resources from heterogeneous sources increased with river hydromorphology quality of the system (Poppe *et al.*, 2016) which allowed to stabilize food webs (Layman *et al.*, 2007a) and support diet-plastic taxa during low resource period (Kupilas *et al.*, 2016). At Ham sur Meuse, scrapers, likely to feed on periphyton, were positioned at the right of the trophic niche closer to the autochthonous benthic resources than the other functional groups as deposit feeders or shredders (Figure 1) centered on the detrital organic matter and bryophytes. This result suggests that some macroinvertebrate taxa had a flexible diet and could consume both allochthonous and autochthonous carbon. Collins and colleagues (2016) stressed that the presence of a functional feeding group does not necessarily indicate the origin of energy used by the community, as shredders can assimilate autochthonous organic matter, whereas scrapers can consume allochthonous carbon. They also highlighted the major role of terrestrial resources and bryophyte for the food web in large tropical and temperate rivers. Few studies reported that bryophytes may contribute to the diet of macroinvertebrates. Our results agree with those of Torres-Ruiz *et al*. (2007) which found that bryophytes was a substantial source of food for macroinvertebrates in spring in the Muscoot River, whereas allochthonous organic matter was the main resource in summer and autumn.

On the other hand, at Waulsort, many consumers were more $\delta^{13}C$-depleted than the potential resources. In anoxic environments, organic matter degradation produces methane (CH_4), which may be used by methanotrophs as source of carbon, in the sediment or the water column (Conrad, 2005). This source of energy can be detected in the freshwater food web with the stable isotope approach, due to the isotopic composition of environmental CH_4 which is heavily $\delta^{13}C$-depleted, with values from -40 to -110‰ in freshwater lakes (Taipale *et al*., 2007). Methanization is well described in lakes, but studies are scarcer in rivers. Methane could nevertheless represent between 1 to 46% benthic net photosynthetic production in gravel beds. Moreover, methanotrophs carbon conversion efficiency (50%) is higher than the one of detrital bacteria (10-30 %; Grey, 2016). Chironomid larvae and caddis flies can present a strongly depleted $\delta^{13}C$ signature as they assimilate methane-derived carbon from methane-oxidizing bacteria in sediments (Deines *et al*., 2007). In our study, four taxa (Chironomidae, Corbiculidae, Corophiidae and Limnephilidae) exhibited more negative $\delta^{13}C$-value than their potential sources of food (Figure 1), which may indicate a contribution of carbon derived from methanization in their diet. Many authors have found evidence of methanotroph organisms contributing in macrophytes, chironomid larvae and their consumers (Sanseverino *et al*., 2012; Agasild *et al*., 2014). Thus, methanotroph organisms could be a complementary

source of energy in the freshwater food-web due to the diversity of primary consumers (Trimmer *et al*., 2012), especially in the case of planktonic-resources diminution.

If the $\delta^{13}C$ range of trophic niche of the macroinvertebrate community at Ham sur Meuse was wider, the $\delta^{15}N$ range was smaller than in Waulsort (Figure 3). The $\delta^{15}N$ range allows quantifying the food chain length of the community (Perkins *et al.*, 2014), which have been recognized to influenced the structure of the community (Post, 2002b). For each trophic level or consumption of prey by a consumer, a proportion of energy (13 to 50%) is lost during assimilation (Andersen *et al*., 2009). A longer food chain than at Waulsort was potentially less efficient notably in case of resources reduction (Dickman *et al.*, 2008) and could destabilize interaction strengths of the food web (Kuiper *et al.*, 2015). Furthermore, energy inefficiencies at multiple trophic positions could be increased when community was dominated by non-native taxa as it is the case in Waulsort. For example, Cross and colleagues (2013) found at the Colorado River a large energy inefficiencies due to consumer-resource mismatches which reduced productivity of the system and increased instability. Native fish could consume only a little part of the most representative invertebrate taxa, the exogenous *Potamopyrgus sp,* which reduced the energy input for the top of the food-web and formed a surplus of invertebrate production.

Facing to a small $\delta^{13}C$ range , a large food chain length at Waulsort and according to the niche overlap theory (Pianka, 1974), we expected an important trophic niche overlap between sympatric potential 'competitors' in the most altered site resulting an overexploitation of some food sources and competition increase. Unexpectedly, the opposite effect was observed with a major trophic niche overlap between sympatric consumers (Figure 4) in the site having more basal resources (Figure 3). Many authors also described no consistent pattern in niche partition in relation with food resources (Correa & Winemiller, 2014) or hydromorphology quality of the river (Kupilas *et al.*, 2016). However, it is important to notice that the availability of the principal food sources consumed by the studied taxa (decomposed organic matter, bryophyte or macroinvertebrate prey) was not directly quantified. And although we observed an enormous drop of phytoplankton at the end of the 90's, the macroinvertebrate community may not lack of resources due to the presence of alternative food. We can also suppose that in the event of resource limitations, the trophic competition increased at Waulsort creating a trophic-niche segregation which forced populations to occupy non-optimal niches (Neto *et al.*, 2017). Furthermore, Flaherty and Ben-David, (2010) found with a modelling approach that some generalist populations can exhibit a smaller trophic niche compared to specialist population following to missing prey items or the spread of the isotopic value food source's (Araújo *et al.*, 2007). On the other hand, some mechanisms for coexistence at the individual level could be plausibly set up to exploit more efficiently food resources (da Silva *et al*., 2017). A large generalist population can hide a subset of specialized individuals utilizing specific trophic niches and developing novel specializations (Pagani-Núñez *et al*., 2016). The reason of the individual specialization has currently received insufficient attention (Araújo *et al*., 2011) but can be induced by inter or intraspecific competition, resource limitation and behavioural plasticity (Svanback & Bolnick, 2007).

Conclusions and caveats

Stable isotope compositions of food web components provide informations on ecosystem functioning. In this study, we highlighted that, (i) due to a potential higher availability of diversified basal resources in the less regulated site, the trophic niche was wider than in the channelized sector, with a contribution of allochthonous detritus and bryophytes at both sites (ii) methanotrophy can contribute to the river food web and (iii) the most disturbed site had the greatest trophic niche, which was potentially less efficient notably in case of resources reduction, and a lower trophic niche overlap between sympatric consumers.

Ce qu'il faut retenir de ce chapitre

Dans le 4ème chapitre, nous étudions l'origine des matières carbonées alimentant le réseau trophique et nous émettons l'hypothèse que les communautés de poissons et de macroinvertébrés de la Meuse française ont été moins perturbées par la diminution des ressources planctoniques qu'en Meuse belge du fait de la diversité des ressources alimentaires alternatives disponibles (périphyton, végétation aquatique, ripisylve…).

Les analyses isotopiques réalisées ont établi que les communautés de macroinvertébrés benthiques des deux sites consomment majoritairement des matières organiques provenant de la ripisylve ainsi que des végétaux aquatiques. Le seston ainsi que le périphyton ne contribuent que très faiblement au réseau trophique. Toutefois, la niche trophique de la communauté semble plus étendue sur la station faiblement anthropisée suggérant que les ressources primaires utilisées par les macroinvertébrés sont plus diversifiées. Toutefois, la contribution des bryophytes dans le régime alimentaire des macroinvertébrés semble assez discutable, notamment en Meuse française où cette ressource est relativement peu présente.

Dans une seconde partie nous avons comparé le recouvrement des niches isotopiques de taxons ayant un régime alimentaire théorique similaire. Le recouvrement des niches trophiques est significativement plus important en Meuse française, ce qui suppose qu'en cas de limitation des ressources trophiques, la compétition alimentaire en Belgique crée une ségrégation des niches forçant potentiellement certains taxons à consommer des ressources alternatives non optimales.

Les deux derniers chapitres sont axés sur l'étude de la niche isotopique des poissons en fonction de leur développement ontogénique. Nous tentons de confirmer qu'en cas de faible disponibilité des ressources planctoniques la compétition trophique intra et inter-stade(s) de développement ontogénique des jeunes poissons est plus importante dans les biefs aménagés pour la navigation.

Chapitre 5

Isotopic half-life and enrichment factor in two species of European freshwater fish larvae: an experimental approach

Avant-propos

Les deux derniers chapitres de cette thèse sont axés sur les relations trophiques de jeunes poissons de l'année, décrites à l'aide d'analyses isotopiques des éléments C et N.

Le 5ème chapitre a pour objectif de mesurer deux paramètres isotopiques dépendant du stade de développement ontogénique de l'individu et de l'espèce étudiée. Des gamètes de deux espèces de cyprins, le gardon et le chevaine (*Squalius cephalus*) ont été récoltés sur des individus sauvages de la Meuse à Namur afin de procéder à une expérience en conditions controlées. Après éclosion et résorption de la vésicule vitelline, les larves ont été nourries avec des nauplii d'*Artemia* jusqu'à l'équilibre isotopique. Ensuite un *shift* alimentaire a été réalisé afin de calculer le facteur d'enrichissement trophique (ou *tissue enrichment factor*, TEF), le temps de demi-vie isotopique (ou *half-life*, HL) ainsi que le ratio d'énergie alloué à la croissance/entretien du métabolisme.

Cette expérience a été menée dans son entierté par le doctorant et « son » équipe, en dehors du stripping des adultes et de l'incubation des œufs effectuée par, et, dans les locaux de Mr Defour J. à Jambes.

L'analyse élémentaire des échantillons a été réalisée à l'Université de Liège (laboratoire d'océanologie) par l'équipe de Lepoint G. Ce chapitre a été publié dans le journal Rapid Communications in Mass Spectrometry.

Latli A, Sturaro N, Desjardin N, Michel LN, Otjacques W, Lepoint G, Kestemont P (2017b) Isotopic half-life and enrichment factor in two species of European freshwater fish larvae: an experimental approach. *Rapid Communications in Mass Spectrometry*, **31**, 685–692

Isotopic half-life and enrichment factor in two species of European freshwater fish larvae: an experimental approach

Abstract

Rationale: Stable isotope ratios of carbon and nitrogen are valuable tools for field ecologists to use to analyse animal diets. However, the application of these tools requires knowledge of the tissue enrichment factor (TEF) and half-life (HL). We experimentally compared TEF and HL in 2 freshwater fish larvae. We hypothesised that chub had a better growth/tissue replacement ratio than roach, due to the use of a food closer to their natural diet.

Methods: We determined the isotopic HL, the TEF and the contribution of growth or metabolic tissue replacement to dynamic isotopic incorporation. After yolk sac resorption, larvae were fed for five weeks with prey similar to their natural diet (*Artemia nauplii*) up to the isotopic equilibrium followed by Chironomid larvae. Stable isotope measurements were done using a continuous flow isotope ratio mass spectrometer coupled to an elemental analyser.

Results: Changes in isotopic composition strongly followed the predictions of exponential growth and time dependent models. Isotopic HL varied between 8.2 and 12.6 days and TEF of nitrogen and carbon ranged from 1.7 to 3.1 ‰ and from -0.9 to 1.2‰, respectively. The incorporation of dietary ^{13}C was more due to the production of new tissue (between 56 and 79%) than to the metabolic process. Chub allocated more energy to growth than roach and the Chironomidae diet contributed more to the consumers' growth than the *Artemia* diet.

Conclusions: Metabolic rates seemed smaller for chub than roach, especially when they were fed with Chironomidae. A Chironomidae based diet would be more profitable to chub, and the high associated growth rate could increase the development of the fish larvae. HL and TEF were in the range of those reported in the literature. These results will be helpful for field based studies, because they can help to increase the accuracy of models.

Introduction

In the last few decades, stable isotope ratios of light biogenic elements have become valuable tools for studying trophic relationships and food web structure (Peterson & Fry, 1987; Layman *et al.*, 2012), and also to estimate the energy content in young-of-the-year fish (or larvae) (Lazo *et al.*, 2010). The carbon stable isotope ratio ($^{13}C/^{12}C$, usually expressed as $\delta^{13}C$) exhibits a weak increase per trophic level and is generally used to track the origin of the carbon source in dietary reconstruction (DeNiro & Epstein, 1978b). In contrast, the $^{15}N/^{14}N$ ratio (expressed as $\delta^{15}N$) of consumers' tissues is often enriched in ^{15}N relative to their diets, thereby revealing both an animal's diet and its trophic level (DeNiro & Epstein, 1981). Combining $\delta^{13}C$ and $\delta^{15}N$ provides quantitative information on resource and habitat, which together define the ecological niche space (Newsome *et al.*, 2007) of species or communities. However, application of stable isotopes in dietary analyses requires knowledge of two major factors, the tissue enrichment factor (TEF, also called discrimination factor) and the isotopic half-life (HL) (Vanderklift & Ponsard, 2003). These two factors can vary significantly in relation to studied ecosystems and species as well as to individual life stage, contributing to error in quantitative mixing model outputs (Zanden & Rasmussen, 2001).

The TEF (also noted Δ) corresponds to the difference between the stable isotope composition of a consumer and its diet, due to isotopic fractionation during metabolic processes (McCutchan *et al.*, 2003). Observed fractionation can fluctuate notably according to the type of tissue analysed, the presence of some classes of compounds (Benner *et al.*, 1987; Focken & Becker, 1998) (for example, lipids, lignin), and the diet or dietary protein content (Zanden & Rasmussen, 2001). Many authors (DeNiro & Epstein, 1978b; Post, 2002b; Vanderklift & Ponsard, 2003; Vander Zanden & Fetzer, 2007) have measured TEFs, and it is usually accepted that the difference between prey and consumer ranges from 1 to 4 ‰ for $\delta^{15}N$ and from 0 to 1 ‰ for $\delta^{13}C$. $\Delta^{15}N$ differs for many groups of organisms and the variance of the estimated enrichment factor must be taken into account in trophic relationship studies (Vanderklift & Ponsard, 2003). Furthermore, TEF value is required to build mixing models, which are used by stable isotope ecologists to estimate the contribution of multiple sources to the diet of a consumer (Wolf *et al.*, 2009).

The isotopic HL is defined as the time it takes for the isotopic composition of a given consumer tissue to reach an intermediate point corresponding to a mid-value between the original diet and the new one. HL can change according to metabolic type (ectotherm versus endotherm), life stage of the consumer, and tissues or taxa analysed (Fry & Arnold, 1982; Herzka & Holt, 2000). HL is also different in growing organisms (Bosley *et al.*, 2002); the more rapid the fish growth, the higher the HL. In the same way, other authors have evaluated the HL to about two days in fish larvae and one year in adults (Bosley *et al.*, 2002; Logan *et al.*, 2006).

To better exploit and validate field data, ecologists have to determine the TEF and HL corresponding to the studied species, in order to estimate the timing of diet shift (Wolf *et al.*, 2009), obtain information on the life history of the target species (Norris *et al.*, 2005),

evaluate time and degree of diet specialisation (Martinez del Rio *et al.*, 2009), and increase the accuracy and realism of mixing models. To meet the requirements of field ecologists, laboratory studies have examined the isotope HL and TEF, and developed models (Wolf *et al.*, 2009) adapted from an exponential growth model (Fry & Arnold, 1982). Hesslein and colleagues (Hesslein *et al.*, 1993) have observed that isotopic incorporation depends on the addition of tissue resulting from growth ('anabolism turnover') and tissue renewal ('catabolism turnover'). Energy from food was allocated in the metabolic process and growth, with a ratio which varied according to the development stage (Lemieux *et al.*, 2003), the type of food, and the environment (notably temperature, which controls biochemical reaction rate in poikilotherm species (Wuenschel *et al.*, 2004)). A study on the warm-water adult zebra fish (*Danio rerio*) demonstrated that metabolic tissue replacement accounts for 68 to 80 per cent of the modification of the isotopic composition following a dietary shift (Tarboush *et al.*, 2006). However, contribution of growth could account for more than 90 per cent for the cold-water red drum larvae (*Sciaenops ocellatus*) (Herzka & Holt, 2000).

Ten years after the call for more laboratory experiments by Gannes and collegues (Gannes *et al.*, 1997), a large number of measurements of incorporation rate have been realised. However, the dynamics of isotopic incorporation mostly been measured on one-compartment models (Martinez del Rio *et al.*, 2009), without dissociating tissue growth and catabolic turnover. Furthermore, the number of experimental studies remains rather low when compared with observational field studies (Logan *et al.*, 2006).

In this study we have selected two cyprinid larvae (young-of-the-year): chub (*Squalius cephalus*) and roach (*Rutilus rutilus*), both common freshwater species widely distributed in Western Europe (Blanck & Lamouroux, 2006; Daufresne & Boët, 2007). Throughout their larval stage, chub and roach mainly feed on zooplankton. However, later in life their diets diverge, with chub starting to feed on benthic invertebrates and roach becoming omnivorous (Garner, 1996). Nevertheless, food acquisition and assimilation are important for both fish for growth and survival, particularly during early stages when individuals are highly vulnerable to competition, food shortage and other perturbations (Nunn *et al.*, 2007a, 2012).

The aim of this paper is to describe a controlled diet-shift experiment conducted on the larvae of *S. cephalus* and *R. rutilus* with two kinds of prey that are close to their natural diets. Firstly, we measured stable nitrogen and carbon isotopes HL and TEF of the fish larvae using an exponential time dependent model (Hobson & Clark, 1992). Secondly, using an exponential growth and time-dependent model (Hesslein *et al.*, 1993), we studied the contribution of metabolic tissue replacement or growth to the variations in isotopic composition of young-of-the-year larvae resulting from the diet shifts. We hypothesised that, during the second diet, chub had a higher 'growth/tissue replacement' ratio than roach, due to the use of a food more in line with their natural diet.

Materials and Methods

Experimental design

Our investigations were conducted in accordance with the guidelines for animal use and care and in compliance with Belgian and European regulations on animal welfare. Adult roach (n=20) and European chub (n=8) were sampled in the Meuse River at the fish pass of La Plante dam (Namur province, Belgium, 50°27'01.9"N ; 4°51'40.6"E) during the spawning period (23–25 April 2015). Roach and European chub gametes were collected by stripping and ova were fertilised with the sperm of multiple males. Eggs were incubated at 12°C under a 12L:12D photoperiod, under static conditions with filtered and UV-sterilised water from the Meuse River. Water was replaced daily. Eggs and yolk sac larvae were collected for isotopic analysis. After yolk sac resorption, approximately 1,000 larvae of each species were distributed between six tanks (110L) at a constant temperature (15°C) and under a constant photoperiod (12L:12D). Water quality was kept stable by a filtration and cooling system, while detritus and uneaten food were siphoned daily. The initial $\delta^{13}C$ and $\delta^{15}N$ of larvae before feeding were determined by sampling three larvae in each tank (t_0). Over five weeks (t_0 to t_5), larvae were fed daily, in excess of five times a day, with freshly hatched *Artemia salina nauplii* ($\delta^{13}C$=-22.7 ± 0.1‰ and $\delta^{15}N$=11.2 ± 0.1‰). From t_5 to t_{10} (five weeks) a diet shift was performed, and larvae were fed daily and slightly in excess with coarsely chopped frozen chironomid larvae ($\delta^{13}C$=-18.1 ± 0.6‰ and $\delta^{15}N$=8.6 ± 0.8‰). We selected these prey because they are close to the diet of cyprinid fish in their natural environment and are isotopically distinct from *Artemia nauplii*. During the dietary shift experiments, three larvae per tank (n=18 per species and per sampling date) were randomly selected each week for isotopic analysis, after 24 hours of food privation for gut clearance. Stable isotope measurements were performed on whole fish. One prey sample was collected daily (n=77).

Fish larvae were anesthetised and killed using an excess of 2-phenoxyethanol (3mL/10L freshwater), measured (total length (TL, ± 1mm), weighed with a microbalance (± 0.1mg), and rinsed with deionised water. Larvae (chub and roach) and diet samples (*Artemia nauplii* and Chironomidae) were dried at 60°C for at least 48 hours and ground into a fine homogenous powder using a mortar and pestle. Due to their small mass, larvae were pooled at t_0 and t_1, and treated individually from t_2 to t_{10}.

Stable isotope ratios measurements were performed via continuous flow—elemental analyser—isotope ratio mass spectrometry (CF—EA—IRMS), using a vario MICRO cube elemental analyser (Elementar Analysensysteme GmBH, Hanau, Germany) coupled to an IsoPrime100 mass spectrometer (Isoprime, Cheadle, United Kingdom). Isotopic ratios were expressed using the international δ notation (Coplen, 2011). Sucrose (IAEA-C6, $\delta^{13}C$=-10.8 ± 0.5‰, mean ± SD) and ammonium sulphate (IAEA-N2, $\delta^{15}N$=20.3 ± 0.2‰, mean ± SD) were used as certified reference materials. Both of these reference materials were calibrated against the international isotopic references, i.e. Vienna Pee Dee Belemnite (VPBD) for carbon and atmospheric air for nitrogen. Standard deviations on multi-batch replicated measurements of lab standards (fish tissues), analysed interspersed among the samples (two lab standards for

15 samples), were 0.1 ‰ for $\delta^{13}C$ and $\delta^{15}N$. Glycine (Merck) was used as an elemental standard and elemental contents were expressed as a percentage of dry mass.

Turnover times and fractionation factor estimations

Firstly, to estimate change in isotopic ratio following the diet shifts, HL were calculated with the time-dependent model adapted from Hobson and Clark (Hobson & Clark, 1992):

$$\delta X_{(t)} = \delta X_{(\infty)} - [\delta X_{(0)} - \delta X_{(\infty)}] e^{-\lambda t} \quad (1)$$

Where $X_{(t)}$ is the isotopic ratio of ^{13}C or ^{15}N in the consumer tissue at time t, $\delta X_{(\infty)}$ is the asymptotic isotopic ratio (‰), $\delta X_{(0)}$ is the isotopic ratio before diet shift (‰) and λ is the turnover rate ($time^{-1}$).

Secondly, based on the growth and time-dependent model adapted from Fry and Arnold (Fry & Arnold, 1982), we evaluated the contribution of growth (k) and metabolism (m) to the ^{13}C isotopic turnover following the diet shifts:

$$\delta^{13}C_{(t)} = \delta^{13}C_{(\infty)} - [\delta^{13}C_{(0)} - \delta^{13}C_{(\infty)}] [w_{(0)} / w_{(t)}]C^{t} \quad (2)$$

Where $w_{(0)}$ is the body mass (g) before the diet shift and $w_{(t)}$ is the body mass at time (t). C represents the metabolic turnover to change in isotope ratio ^{13}C.

As young-of-the-year fish grow exponentially, we can assess growth rate (k_g, expressed in day^{-1}) and the metabolic contribution (k_c) to isotopic turnover following the equation proposed by Hesslein and colleagues (Hesslein *et al.*, 1993):

$$k_g = \ln [w_{(t)} / w_{(0)}] / t \quad (3)$$

With t the time (day) between the two measures.

$$k_c = \lambda - k_g \quad (4)$$

Finally, according to Martinez del Rio and Anderson-Sprecher (Martínez del Rio & Anderson-Sprecher, 2008), we used a nonlinear least squares fitting procedure (Seber & Wild, 1989) and isotopic HL to estimate the parameters of equations 1, 2 and 3 using the following equations:

$$HL = \ln(2) / (k_c + k_g) \quad (5)$$

Tissue fractionation factors were calculated for the two diet shifts (*Artemia* sp. or Chironomidae) according to the following formula:

$$TEF = \delta X_{(\infty)\ consumer} - \delta X_{diet} \quad (6)$$

With δX_{diet} the mean diet isotopic composition.

Results

The isotopic composition of both species displayed a strong temporal pattern during the dietary shift under controlled laboratory conditions. Chub and roach larvae grew by 2.4g and 2.0g respectively in the five weeks before the dietary shift, and by 11.6g and 7.5g in the five weeks after (Table 1).

Table 1: Mean total length (mm) and mean growth (g) of chub and roach larvae during the dietary shift experiment.

	Time	Total length (mm)		Growth (g)	
	(weeks)	Mean	SE	Mean	SE
Chub	0	7.9	±0.3	0.4	±0.02
	5	14.9	±0.2	2.8	±0.6
	10	25.0	±0.6	14.4	±4.7
Roach	0	6.2	±0.4	0.1	±0.01
	5	14.8	±0.3	2.1	±0.1
	10	23.2	±0.8	9.6	±1.0

The time-dependent model (Hobson & Clark, 1992) performed adequately with our data, as goodness-of-fits were comprised between 0.78 and 0.98 (Figure 1 and Figure 2), except for the $\delta^{15}N$ for the first feeding period (Figure 2). Extrapolated equilibrium curves were close to the mean larval isotope values at t_5 or t_{10}, suggesting that larvae performed a complete turnover at the end of each diet experiment.

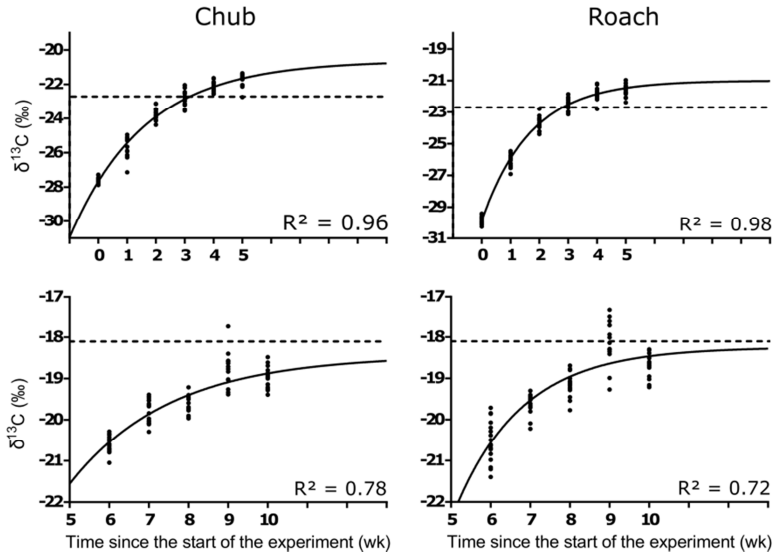


Figure 1: Carbon isotopic values (mean ± SE) of chub (left) and roach (right) larvae, relative to laboratory experiment time (week), during the first *Artemia* diet (top) and the second Chironomidae diet (bottom). The curve (solid line) represents the best-of-fit nonlinear regressions using Hobson and Clark's (1992) model (n=114), and the dashed line represents the mean diet isotopic composition (n=39).

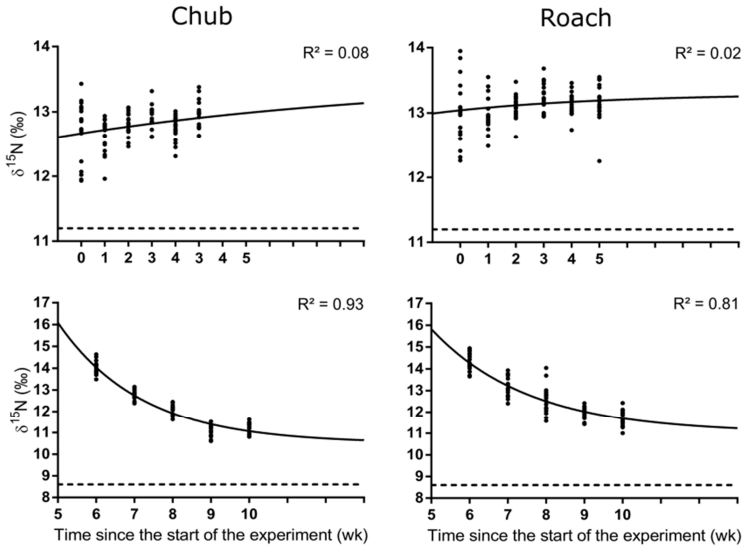


Figure 2: Nitrogen isotopic values (mean ± SE) of chub (left) and roach (right) larvae relative to lab experiment time (week), during the first *Artemia* diet (top) and the second Chironomidae diet (bottom). The curve (solid line) represents the best of fit nonlinear regressions using Hobson and Clark's (1992) model (n=114), and the dashed line represents the mean diet isotopic composition (n=39).

Carbon isotopic HL were relatively brief, ranging between 8.2 and 12.7 days (Table 2), and showed a relative homogeneity between diet and species. Nitrogen isotopic HL were also found in this range for the second diet (10.6 and 12.4 days for roach and chub respectively). However, nitrogen HL calculated for the first diet were certainly overestimated, with values of 27.6 days for roach and 72.7 days for chub. Moreover, the model poorly described the temporal evolution of $\delta^{15}N$ in larvae fed with *Artemia* sp. in both species (R^2= 0.02 for roach and 0.08 for chub).

Table 2: Half-life (HL) and tissue enrichment factor (TEF) estimations, calculated using nonlinear regressions of carbon and nitrogen stable isotopes (time-dependent model adapted from Hobson and Clark (1992) following diet shift from *Artemia* sp. to Chironomidae.

		First diet (*Artemia* sp.)					Second diet (chironomidae)				
Element	Specie	R^2	Half-life (days)	Asymptotic isotopic ratio (‰) Mean	SE	Tissue enrichment factor (‰)	R^2	Half-life (days)	Asymptotic isotopic ratio (‰) Mean	SE	Tissue enrichment factor (‰)
$\delta^{13}C$	Chub	0.96	12.7	-20.6	± 0.03	2.1	0.78	12.4	-18.4	± 0.05	-0.3
	Roach	0.98	8.2	-21	± 0.02	1.7	0.72	8.2	-18.2	± 0.04	-0.1
$\delta^{15}N$	Chub	0.08	72.7	13.5	± 0.8	2.3	0.93	10.6	10.5	± 0.03	1.9
	Roach	0.02	27.6	13.3	± 0.14	2.1	0.80	12.4	11	± 0.06	2.4

Ratios between the contribution of metabolism and growth (k_c/k_g) for $\delta^{13}C$ were smaller for the Chironomidae diet than for the *Artemia* diet (Figure 3) and roach had a higher ratio than Chub. Chub k_g accounted for 61 per cent during the first diet and 79 per cent during the second diet of the $\delta^{13}C$ incorporation, while roach k_g were slightly lower (56 and 71 per cent respectively).

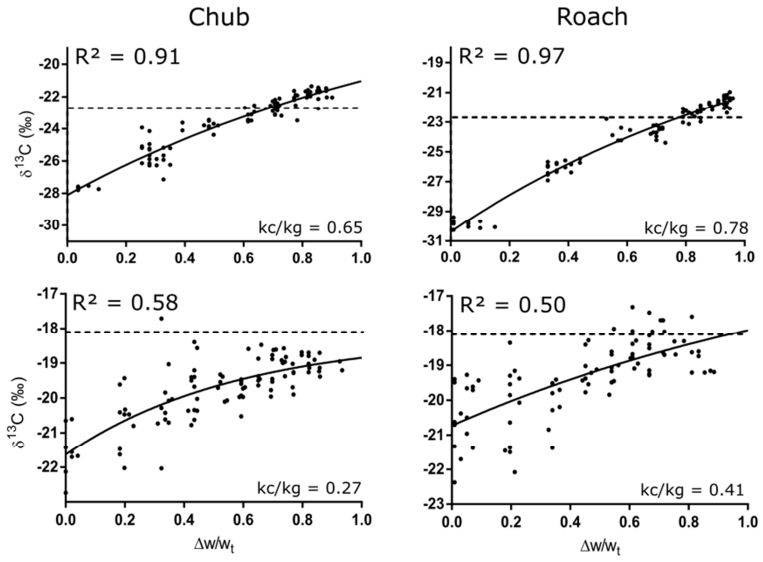


Figure 3: Carbon isotopic values (mean ± SE) of chub (left) and roach (right) larvae relative to relative mass change (Δ w/w_t), during the first *Artemia* diet (top) and the second Chironomidae diet (bottom). The curvature of the solid line (n=114) decreases if the contribution of the growth (k_g) to isotopic incorporation increases. The dashed line represents the mean diet isotopic composition (n=39).

Isotopic composition of the *Artemia* diet proved to be relatively constant, because variability on this parameter was comparable to our instrument's analytical precision (SE=0.1‰ for carbon and nitrogen). The variation in isotopic composition in Chironomidae was higher but still moderate (SE=0.6 and 0.8‰ respectively for carbon and nitrogen). These differences in variability between the two food sources did not affect the quality of the model predictions, with a high R^2 during each period of the experiment.

TEFs were relatively homogenous between diet and species (Table 2). $\Delta^{15}N$ were comprised between 2.1 and 2.3‰ for the *Artemia* diet and between 1.9 and 2.4‰ for the Chironomidae diet. $\Delta^{13}C$ varied widely, and were positive for the *Artemia* diet (2.1‰ for chub and 1.7‰ for roach) and negative for the Chironomidae diet (-0.3‰ for chub and -0.1‰ for roach).

Discussion

Due to an exponential growth, ectotherm young-of-the-year chub and roach exhibited isotopic incorporation patterns that followed theoretical models (McCutchan *et al.*, 2003). As observed in ectotherm larvae, the measured isotopic HL were small and isotopic incorporation was mainly due to growth (Herzka & Holt, 2000; Gajdzik *et al.*, 2015). Variation of fish isotopic composition during the experiment strongly matched with the exponential time-dependent model (Hobson & Clark, 1992), and goodness-of-fits were higher than 0.72 except for the nitrogen composition during the first feeding period (Table 2). The model poorly described this part of the experiment because the $\delta^{15}N$ values of both consumers remained unchanged from t_0 to t_5 (Figure 2). This can likely be explained by the low variations between initial and final diets. Differences in isotopic value between prey and consumers at t_0 were roughly

equivalent to the fractionation factor, making any attempt at calculating turnover times irrelevant.

Difference in tissue enrichment factor between diets

Even though TEFs are commonly used by scientists for quantifying contribution of alimentary sources in the diet of consumers, they vary greatly according to the considered element and sample tissue, as well as physiology of the studied species (Vanderklift & Ponsard, 2003). A meta-analysis by Le Vay and Gamboa-Delgado (Le Vay & Gamboa-Delgado, 2011) reported a considerable variability in aquatic larvae and post-larvae $\Delta^{13}C$ and $\Delta^{15}N$ observed under laboratory conditions, from 0.4 to 4.1‰ for carbon and from 0.1 to 5.3‰ for nitrogen. The TEFs gathered in this meta-analysis come from various organisms, mainly crustacean larvae. Only one was measured in post-larval marine fish fed with natural or artificial food. These large ranges of observed TEFs nevertheless highlight the requirement of laboratory experiments to measure representative TEFs that can be efficiently applied to environmental or ontogenetic studies.

One review (Caut *et al.*, 2009) proposed a global evaluation of adult fish isotopic TEF around 1.7‰ for $\delta^{13}C$ and 2.5‰ for $\delta^{15}N$; the estimations were mostly in line with our results for $\Delta^{15}N$ (between 1.9 and 2.4‰), as well as for $\Delta^{13}C$ during the first diet (between 1.7 and 2.1‰). However, for the period of the second diet, prey had a lower $\delta^{13}C$ ratio compared to consumers (-0.3 to -0.1‰). Less common than positive values, negative $\Delta^{13}C$ were reported by McCutchan *et al* (McCutchan *et al.*, 2003), with a minimum observed value of to -2.7‰ (Buckeye pupae fed with Plantago). As lipids are more ^{13}C-depleted than proteins, negative TEF could be linked with the lipid content in the analysed tissue if consumer tissues were richer in lipid than their diet, which was not the case in our experiment. Another explanation could result from the amino acid concentrations between the prey and the consumer, which influence TEF (Martinez del Rio *et al.*, 2009); however, this mechanism has been poorly studied (Kim *et al.*, 2012).

TEF differences between consumers were small, with a maximum close to 0.5‰, possibly due to common diet, common requirements (i.e. larval growth phase) and their taxonomic proximity. TEFs observed between consumers were higher in the literature for the same type of diet, for example $\Delta^{15}N$ of marine crustaceans fed with *Artemia* varied between 0.1 and 2.5‰ (Le Vay & Gamboa-Delgado, 2011). For both consumers, we also noticed that the $\Delta^{13}C$ variation was higher than the $\Delta^{15}N$ in this study (contrary to the literature ; Le Vay & Gamboa-Delgado, 2011) and depended mainly on the type of diet (Table 2): $\Delta^{13}C$ differences were 1.8 to 2.4‰, greater for *Artemia* sp. than for Chironomidae diet. This variation was smaller for $\Delta^{15}N$, between 0.2 to 0.4‰. In the literature, $\Delta^{15}N$ and $\Delta^{13}C$ measured for the same taxa can vary with diet type from 0.8‰ to 6.6‰ and 0.4 to 7.0‰ respectively (McCutchan *et al.*, 2003; Le Vay & Gamboa-Delgado, 2011).

Difference in isotopic incorporation rate

With the exception of the $\delta^{15}N$ HL during the first feeding period, isotopic incorporations fluctuated between 8 and 13 days according to species and diet. These results were close to the results reported in similar studies (Herzka & Holt, 2000; Bosley *et al.*, 2002). For example, Bosley and colleagues (Bosley *et al.*, 2002) determined HL in muscle tissue for three marine fish larvae species of between 1 to 17 days for carbon and 2 to 19 days for nitrogen.

In a literature review, Vander Zanden and colleagues (2015) proposed an HL evaluation method for ectotherm vertebrates based on allometric relationships between organism weight and isotopic incorporation. With our data, the isotopic HL estimations were comprised between 36 and 39 days for the first diet, and 51 and 57 days for the second diet (respectively for roach and chub). These values are longer than those estimated in our study. The difference may be due to the temperature at which the larvae in our study were reared and hence to high growth rates, which is not taken into account by the model. Many authors (Bosley *et al.*, 2002; Witting *et al.*, 2004) have highlighted a significant effect of temperature on isotopic HL, notably in fast growth organisms such as larvae. Furthermore, growth rate influences isotopic HL, since lower growth rate increases the isotopic HL while rapidly growing species have a short HL due to a high metabolic rate (Fry & Arnold, 1982). Even though growth rate varies widely according to developmental stage, this parameter was not taken into account by the models of Vander Zanden *et al* (2015). In our study, young-of-the-year fish allocated a large amount of energy in growth (k_c) and tissue production rather than metabolic turnover (k_g) (Figure 3). Similarly, Zuanon and colleagues (2006) estimated $\delta^{13}C$ HL for Nile tilapia (*Oreochromis niloticus*), a large freshwater fish, around 52.5 to 66.5 days for larvae, and 120 days for juveniles. Turnover of adult whitefish could be superior to one year (Hesslein *et al.*, 1993), reflecting the reduction of growth and slowing of metabolism compared to younger individuals.

Contribution of growth to incorporation of dietary ^{13}C in consumer tissues

The contribution of growth (between 56 to 79 per cent) to ^{13}C incorporation was comparable with the literature. A similar study on a cold-water red drum larvae (*Sciaenops ocellatus*) (Herzka & Holt, 2000) evaluated the growth contribution at 90 per cent, but this trend could be inverted for larger adult fishes such as shark (Kim *et al.*, 2012).

Chub allocated more energy to growth than roach, which had a higher metabolic rate (Figure 3). Chub tissue production accounted for 61 per cent in the $\delta^{13}C$ incorporation during the first part of the experiment and for 79 per cent after the diet shift, while roach values were slightly lower (56 and 71 per cent respectively). In both cases, the ratio was higher when organisms were fed using the second rather than the first diet. The Chironomidae diet facilitated assimilation and reduced metabolic processes for both study species (Figure 3). This diet benefited both fish larvae, although the Chironomidae diet was more in line with the natural food of chub, whose juvenile mainly consume macroinvertebrates, than roach, which are

omnivorous[42]. In a natural environment, a Chironomidae-based diet would be more profitable to chub, and the high associated growth rate could increase the development of the fish larvae and their chances of survival (Yúfera & Darias, 2007).

Conclusion and caveats

This experimental study evaluated the isotopic HL and TEF of two freshwater cyprinid larvae fed using two different regimes close to their natural diets. For both species, HL was short and isotopic incorporation rates were mostly due to the prompt production of new tissue during the early stage of life. Carbon and nitrogen TEFs were in the range of those reported in the literature. While they differed slightly according to consumer species, due to analogous requirements (i.e. larval growth phase) and their taxonomic proximity, the $\Delta^{13}C$ observed were very different between the two experimental diets. Metabolic rate seems smaller for chub than for roach, especially when fed with Chironomidae, which can benefit to chub in its natural environment. Based on these results, we can make some recommendations to open field researchers for increasing the accuracy and realism of their models. First, it is important to precisely determine the developmental stage of the consumers, because HL of larvae is shorter than adults and the HL observed may not follow the modelled curves from the literature (Vander Zanden *et al.*, 2015). Secondly, open field researchers have to use a TEF that is estimated on the studied species and their potential food sources that can be found in the natural environment. In the same way, HL has to be evaluated in experimental conditions closed to the natural environment, for example for ectothermic species in which metabolic activities are directly linked with temperature (Bosley *et al.*, 2002). Thirdly, laboratory measurements must be taken with caution; consumers are generally located in an ideal position in terms of food availability and environmental stability. In an open field, life conditions might be more difficult with less food available, which leads to a lower growth rate and slower HL than in the laboratory.

Ce qu'il faut retenir de ce chapitre

Dans le 5ème chapitre, nous avons pour objectif de mesurer deux paramètres isotopiques, le taux de fractionnement (tissue enrichment factor ou TEF) ainsi que le temps de demi-vie isotopique (half-life or HL). Ces métriques dépendent du taxon étudié ainsi que du stade de développement ontogénique et de la vitesse de croissance de l'organisme. Une définition précise de ces valeurs contribue à la construction de modèles mixtes permettant d'estimer le régime alimentaire des consommateurs sur la base des valeurs isotopiques des proies potentielles. A l'aide d'une expérimentation contrôlée de shift alimentaire, nous évaluons le TEF et le HL de deux espèces de poissons post-résorption de la vésicule vitelline.

L'expérience a permis de mesurer précisement les paramètres isotopiques pour les deux taxons étudiés. Le temps de demi-vie isotopique est très court (entre 8,2 et 12,6 jours) car les organismes allouent une part importante (entre 56 et 79%) de l'énergie à la production de nouveaux tissus. Le fractionnement isotopique de l'azote et du carbone (respectivement de 1,7 à 3,1 ‰ et de -0,9 à 1,2 ‰) est assez variable mais proche des valeurs constatées dans la littérature.

Enfin le régime alimentaire composé de Chironomidae permet aux deux espèces d'allouer environ 15% d'énergie en plus à la croissance qu'avec un régime composé d'*Artemia sp*.. Il semblerait également que le chevaine ait une croissance légèrement plus rapide que le gardon.

Les paramètres mesurés seront utilisées dans le chapitre suivant pour estimer l'origine des ressources trophiques assimilées par les poissons en fonction de leur stade de développement.

Chapitre 6

River habitat homogenization enhances trophic competition and promotes individual specialization among young-of-the-year fish

Avant-propos

Le 6ème chapitre a pour objectif de modéliser la niche isotopique de 4 espèces de poissons à divers stades de developpement ontogénique en cas de faible disponibilité de ressources planctoniques. Nous cherchons à évaluer l'influence de la régulation hydromorphologique de la Meuse sur la compétition intra- et inter-spécifique mais également intra et inter-stade de développement.

L'inventaire, les nombreuses déterminations et la préparation des échantillons ont été réalisés par le doctorant et « son » équipe. L'analyse élémentaire des échantillons a été réalisée à l'Université de Liège (laboratoire d'océanologie) par l'équipe de Lepoint G. Le doctorant a effectué l'entierté de l'analyse des données et d'interprétation des résultats ainsi que la rédaction de ce chapitre.

Ce chapitre a été récemment accépté et sera publié prochainnement dans la revue Freshwater Biology.

Latli A, Michel LN, Lepoint G, Patrick K. River habitat homogenization enhances trophic competition and promotes individual specialization among young-of-the-year fish. Freshwater Biology. *Accepted august 2018.*

River habitat homogenization enhances trophic competition and promotes individual specialization among young-of-the-year fish

Summary

In large rivers, fish ontogenic development success is mainly influenced by resource availability and by the possibility of species to adapt their diet (*i.e.* trophic niche). Humans have drastically modified freshwater habitats, notably for navigation purposes. Such modifications may reduce food availability for young of the year (YOY) fish and, consequently, influence their ability to reach the adult age.

In the Meuse River, decrease of fish abundance is thought to be linked to a drastic reduction of phytoplankton biomass. In this context of decreasing phytoplankton biomass, we studied trophic niches of three cyprinid species (common bleak *Alburnus alburnus,* chub *Squalius cephalus,* and roach *Rutilus rutilus*) and one percid species (European perch *Perca fluviatilis*) at various stages of development, using stable isotope analysis in order to compare intra- and interspecific competition between sites differing in degree of channelization.

Two reaches of the Meuse River differing by their degree of regulation were investigated. We hypothesized that habitat homogeneization would (i) decrease food resource availability and diversity and (ii) increase trophic competition, particularly among earlier ontogenic stages, and promote individual specialization.

Our study provides evidence that in the context of low planktonic biomass, most YOY relied on benthic food sources. Furthermore, the Meuse River flow and depth regulation significantlty impacted the abundance and species richness of YOY. In the heavily channelized reach, between-stages competition and low resource diversity lead to an increase in diet partitioning between cyprinid larvae, as well as consumption of non-optimal energetic food sources such as aquatic vegetation in part of individuals.

On the other hand, in the less channelized reach, larvae displayed a generalist feeding habit focusing on high energy content prey such as different taxa of macroinvertebrates, suggesting that the diversity of habitat reduces the food competition within and between stages.

Introduction

Pianka (1981) developed a theory popular among ecologists describing the trophic competition between species as the proportion of overlap between their trophic niches. In most cases, when resources and environmental variability decrease, trophic niche overlap tends to increase, which could lead in the most severe situations to competitive exclusion. This typically happens when introduced taxa occupy a new biotope and out-compete their trophic competitors (Ward & Ricciardi, 2007). This is the case in freshwater systems where exotic Dreissenidae mussels (*Dreissena polymorpha* and *Dreissena bugensis*) or Corbiculidae have been shown to reduce populations of other large filter-feeding taxa such as Sphaeriidae and Unionidae (Marescaux *et al.*, 2016). However, if food is abundant, two species could share the same resources without negatively impacting each other (Pianka, 1974). For example, omnivorous fish suffer less from river regulation and habitat destruction than fish having more specialized diets (Aarts *et al.*, 2004; Latli *et al.*, 2017a).

Although food web models are traditionally used to determine trophic interactions between species, several studies have shown that dietary variation may occur within populations or species (Bolnick *et al.*, 2003). Indeed, a generalist species or population consuming a large range of resources may be composed of many individuals specialized on small subsets of food items that differ among individuals. These individual specialists could play their own ecological roles in terms of trophic relationships and habitat use (Yurkowski *et al.*, 2016). Trophic individual specialization (IS) is influenced by increase of trophic competition (intra and/or interspecific), prey diversity and/or abundance, and predation pressure (Araújo *et al.*, 2011). According to the optimal foraging theory (MacArthur & Pianka, 1966), in a system with unlimited food resources, consumers may share preferred resources, decreasing the IS of the population. In contrast, decreasing trophic resources may result in a higher intraspecific competition for the preferred diet. Scarcity of preferred items could in turn force consumers to add alternative resources to their diets, increasing the degree of IS (Kernaléguen *et al.*, 2015).

IS has been well documented for species living in a large number of ecosystems (Araújo *et al.*, 2011), but food web studies have rarely taken into account the ontogeny of individuals, which implies the assumption that food resources are more or less similar for all life stages (Rudolf & Lafferty, 2011). However, trophic interactions develop during the ontogeny of numerous species, with crucial consequences for populations but also for the entire food web (Nakazawa, 2015). The large majority of species with larvae feeding autonomously (invertebrates, fish, amphibians) have at least one diet shift in their early life. In freshwater, the majority of young fish larvae preferentially consume small zooplankton as rotifers, and small cladocera, which are the optimal diet in terms of cost/benefit ratio after yolk sac resorption (Nunn, Harvey, & Cowx, 2007). This diet can be completed by small insects and phytoplankton. The diet of older larvae is generally more diversified: juveniles typically shift to benthic macroinvertebrate prey, with an herbivory complement according to the species,

when fin development enables greater swimming performance (Nunn, Tewson, & Cowx, 2012).

As many European rivers, like the Rhone, Danube and Rhine, the Meuse River has been heavily regulated for navigation and flood control, mainly in the Belgian section (Descy, 2009). River channelization and riparian land use reduce the inputs of terrestrial matter usable by the macroinvertebrate community (Lecerf *et al.*, 2012) while dams homogenize habitats by modifying erosion and sediment transport and deposition (Aarts *et al.*, 2004). In the deepened sections of regulated rivers, the development of benthic primary producers has been reduced by light limitation and habitat has been altered by removal of gravel deposits and macrophyte stands. By contrast, habitats of the French section of the Meuse River have been less disturbed, conserving their ecological functions and biodiversity. The shallowness of the French section of the river allows the development of diverse aquatic and subaquatic vegetation, from periphyton to helophytes and hydrophytes. The riparian zone is quite well developed and contributes to increased habitat heterogeneity (Descy, 2009).

A major event in the recent history of the Meuse River was the establishment of non-native filter-feeding bivalves, dreissenid and corbiculid mussels, which contributed to reduce the phytoplankton and zooplankton biomass by 85% over a period of 15 years (Pigneur *et al.*, 2014). As in many European and American freshwater ecosystems (Smith, Higgins, Vander Zanden, Joppa, & Vadeboncoeur, 2011, Ward & Ricciardi, 2007), the invasive filter-feeders have impacted most biota in the Meuse River, from plankton to piscivorous fish (Latli *et al.*, 2017a). However, the impact on fish communities varied according to the degree of channelization. In the Belgian part of the river, the biomass of some species such as roach (*Rutilus rutilus*), which dominated the community during the 90's, was reduced by 85%, mainly as a result of the collapse of the water column resources (Otjacques *et al.*, 2015, 2016). On the other hand, in the less regulated part of the Meuse River in France, the stock of roach remained constant (Alonso *et al.*, 2014).

In this study, we used stable isotopes to compare the trophic ecology of differing developmental stages of four fish species in two differently regulated of the Meuse River, in a context of low phytoplankton availability. We hypothesized that the habitat heterogeneity in the less channelized reach would offer greater food resource availability and diversity, which would increase the abundance of young of the year fish (YOY). We delineated the diet of fish by ontogenic stages to identify the alternative exploited resources and we hypothesized that trophic competition would be stronger among earlier ontogenic stages, with a greater degree of individual specialization in the channelized reach.

Materials and Methods

Study area

The River Meuse rises on the Langres plateau in North-Eastern France, flows through Belgium and Netherlands, and ends up in the Dutch delta after joining the Lower Rhine. The total length of the river is close to 925 Km for a catchment area of 36,011 km². The main characteristics of the river basin and of the river itself were summarised by Descy in Tockner, Uehlinger, & Robinson (2009). The present study was conducted in two reaches of the River Meuse located 469 and 488 km from the source respectively (table 1). The first site (France) is not channelized and navigation is not allowed. The flow is controlled by old-fashioned weirs which generally maintain shallow and fast-flowing reaches allowing the development of aquatic and subaquatic mosses and higher plants. The bank is near-natural in most stretches and the riparian zone is well developed (Ham sur Meuse; N 50° 6' 36", E 4° 46' 49). The second site (in Belgium) is a heavily channelized reach allowing navigation of 1600 tons barges. The water level is regulated by automatic weirs which maintain a relatively high water depth. Frequent and heavy dredging of the river bed as well as concrete and stone banks considerably reduce the development of aquatic and riverine vegetation as well as habitat heterogeneity (Waulsort; N 50° 12' 56", E 4° 49' 37").

Table 1: Physical description of the two sampling sites

Site	**Distance from source** (km)	**Catchment** (km2)	**Chanel width** (m)	**Water discharge** (annual average $m^3.s^{-1}$)	**Altitude** +/-5 m	**Slope** (/1000)
Ham / Meuse	469	10110	100	148	105	0.13
Waulsort	489	10584	120	152	95	0.25

During the last 25 years on the French and Belgian River Meuse, water temperature increased close to 1°C and the phytoplankton biomass decreased (- 85%; figure 1) as well as orthophosphate, nitrate and suspended mater concentrations (Latli *et al.*, 2017). The zooplankton followed the same trend: during the 1990s the mean abundance of Rotifera was between 300 and 500 ind.L^{-1} through the summer with maxima close to 4000 ind.L-1. After 2010, the maximal abundance was lower than 100 ind.L^{-1} (Viroux L., *unpublished data*).
Benthic macroinvertebrate abundance is similar in the two studied sites. The species richness is slightly higher at Waulsort (28) than at Ham sur Meuse (25) mainly due to exotic taxa which represent more than 80% of the sampled organisms. In the channelized section in Belgium, the benthic invertebrate assemblage is dominated by crustaceans (e.g. Asellidae, *Chelicorophium sp*. and *Dikerogammarus sp*.), molluscs (e.g. Corbiculidae, *Dreissena polymorpha*…) and Oligochaetes. Pigneur *et al*. (2014) reported that invasive filter-feeders can reach densities between 50 to 900 individuals by m². In the French site, we found many taxa with preferences for fast-flowing conditions (e.g. Ephemeridae, Coleoptera and Diptera).

The number of scrapers strongly has increased in France in relation with the decrease of the phytoplankton, which resulted in an improvement of water transparency, promoting periphyton and macrophyte growth in the shallowest parts of the river (Latli *et al.*, 2018).

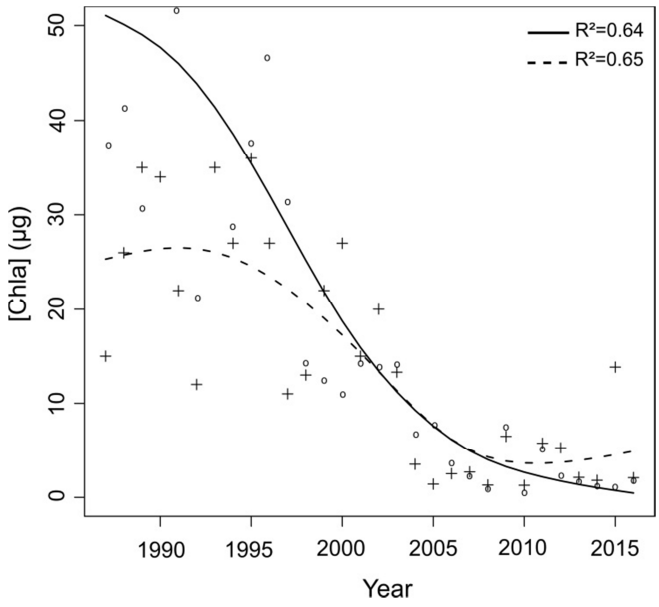


Figure 1: Long-term variation in the annual mean values of Chlorophyll-a ($\mu g.Ll^{-1}$) in the Meuse River between 1987 and 2016. Temporal trends were modelled using a Generalized Additive Model with residual autocorrelation structure. Solid line and dots correspond to Ham-sur-Meuse (France) and dashed line and crosses to Waulsort (Belgium). (Data sources: Water Agency Rhin-Meuse, Public Service of Wallonia and WAter CONtrol DAta system for hydrology and water management).

Sampling and isotope measurement

Sampling protocol

Potential food sources and fish were sampled at both sites every two weeks from April to September in 2013 and 2014. Aquatic vegetation (algae, bryophytes, hydrophytes, periphyton), terrestrial vegetation (bank and litter), planktonic resources, macroinvertebrates (Diptera, Ephemeroptera, Crustacea…) and young of the year fish were sampled as potential food sources (N=591). Macroinvertebrates were sampled with a Surber sampler (mesh size 500 µm) along the banks and by scuba diving in the channel. By successive filtration, we separated planktonic resources into two potential food sources according to their sizes, from 0.6 to 30 µm for fine particulate organic matter and 30 to 150 µm for coarse particulate organic matters. Thirty µm is the theoretical upper size limit of consumable preys by the invasive mollusc *Cobicula fluminea* (Way *et al.*, 1990).

Every two weeks, 40 sampling points were randomly selected in the same part of the reach where potential food sources were collected. Young of the year (YOY) fish were caught using the point abundance sampling by electrofishing (PASE) approach from a boat along the banks, with a 7KW generator delivering a continuous current (150 - 300V at 3A) as proposed

by Copp (2010). Electrofishing was also carried out for sampling adult fish along banks by boat in a large type of habitat over a distance of 800−1000 m. We used a more powerful generator (400 V at 5A, DEKA 7000) to maximise the catch efficiency of large individuals.
Fish were anesthetized and sacrificed using an excess of 2-phenoxyethanol (3mL/10L freshwater) according to ethical requirements, then rinsed with deionized water and frozen in an Eppendorf. All the fish were identified at the specie level using determination key (Pinder, 2001). . Individuals were grouped into three classes (larvae, juvenile and adult), according to their morphological development. We considered as larvae the newly hatched fish with no remaining yolk sac and with dorsal fin rays in development and juvenile individuals with fins sufficiently well developed to allow swimming in open water (see Pinder, 2001 for more information). We considered as adult specimens which have more than one year. The term YOY includes individuals at the larval and juvenile stages.

A total of 8162 fish (7914 YOY and 248 adults) from 20 species were caught and identified. Common bleak (*Alburnus alburnus*), chub (*Squalius cephalus*), roach (*Rutilus rutilus*) and European perch (*Perca fluviatilis*) represented 78% of the total individual sampled. Isotopic analyses were carried out only on these four species, In each site and for every sampling dates, whenever possible, we randomly selected 30 YOY per species for isotopic analysis (common bleak: N=214, chub: N=635, roach: N=652 and European perch: N=101). After measuring the total length to the nearest mm, samples of lateral muscle tissue of each fish were used for stable isotope analysis. Each individual was dried individually at 60°C for at least 48 h and ground into a homogenous fine powder using a mortar and a pestle. Stable isotope ratios measurements were performed via continuous flow - elemental analysis - isotope ratio mass spectrometry at University of Liège, using a vario MICRO cube elemental analyser (Elementar Analysensysteme GmBH, Hanau, Germany) coupled to an IsoPrime100 mass spectrometer (Isoprime, Cheadle, United Kingdom). Isotopic ratios were expressed using the widespread δ notation (Coplen, 2011). Sucrose (IAEA-C6, $\delta^{13}C$ = -10.8 ± 0.5‰, mean ± SD) and ammonium sulphate (IAEA-N2, $\delta^{15}N$ = 20.3 ± 0.2‰, mean ± SD) were used as certified reference materials. Both of these reference materials are calibrated against the international isotopic references, *i.e.* Vienna Pee Dee Belemnite (VPBD) for carbon and Atmospheric Air for nitrogen. Standard deviations on multi-batch replicate measurements of lab standards (fish tissues) analyzed interspersed among the samples (2 lab standards for 15 samples) were 0.1 ‰ for $\delta^{13}C$ and 0.3 ‰ for $\delta^{15}N$.

Isotope metrics

For the twelve fish groups (4 species and 3 stages) composed at least by 5 individuals, isotopic niche parameters were computed using the SIBER package for R (Jackson *et al.*, 2011). SIBER was used to generate bivariate standard ellipses that represent core isotopic niches of consumers, as well as convex hulls that comprise all individual of a $\delta^{13}C$ and $\delta^{15}N$ isotope bi-plot (Layman *et al.*, 2007a). Areas of these ellipses were estimated using an computation method designed to minimise effects of small and/or uneven sample size (SEA_C,

Jackson *et al*. 2011). The cumulative overlap between ellipses of the different fish groups illustrates the potential trophic competition among taxa at the site where samples were collected.

We calculated the contributions of potential food sources to each age class of each species' diet with the R-software (R 3.4 version, R Development Core Team, 2015) using the package "MixSIAR" (Stock & Semmens, 2013). The isotopic variations of potential food sources were characterized by the mean of the taxa family (± SD) and the abundance of each taxon analysed (appendix 12). The MixSIAR models were constructed using Trophic Enrichment Factors (TEF) determined previously by the authors during a controlled experiment targeted on YOY of the studied species (Latli *et al.*, 2017b) and with the formula proposed by Caut *et al*. (2009) for adults. To reduce the number of potential food sources in the model, we pooled prey types if stable isotope values were not statistically different as proposed by Phillips *et al*. (2014).

In addition to age class analysis, MixSIAR was also used to compute relative prey contribution to the diet of each individual fish. This output was subsequently used to calculate the individual trophic specialization of each fish species and age class using the method developed by Araújo *et al*., (2007) and Bolnick *et al*. (2002) with the "RInSp" package (Zaccarelli *et al.*, 2013). For each fish group, we estimated the Total Niche Width (TNW, a measure of population-level variance in diet) as the sum of diet variability within individuals (or within-individual component, WIC) and diet variability between individuals (between-individual component, BIC). A smaller WIC than BIC is generally related to a specialist population. The ratio between WIC and TNW measured the degree of intra-population foraging specificity (also called individuality). A ratio close to 1 indicates that all individuals exploit the complete range of the population's niche, as opposed to populations that comprise individuals having narrower isotopic niches than the population which are considered as individual dietary specialists.

Statistical analysis

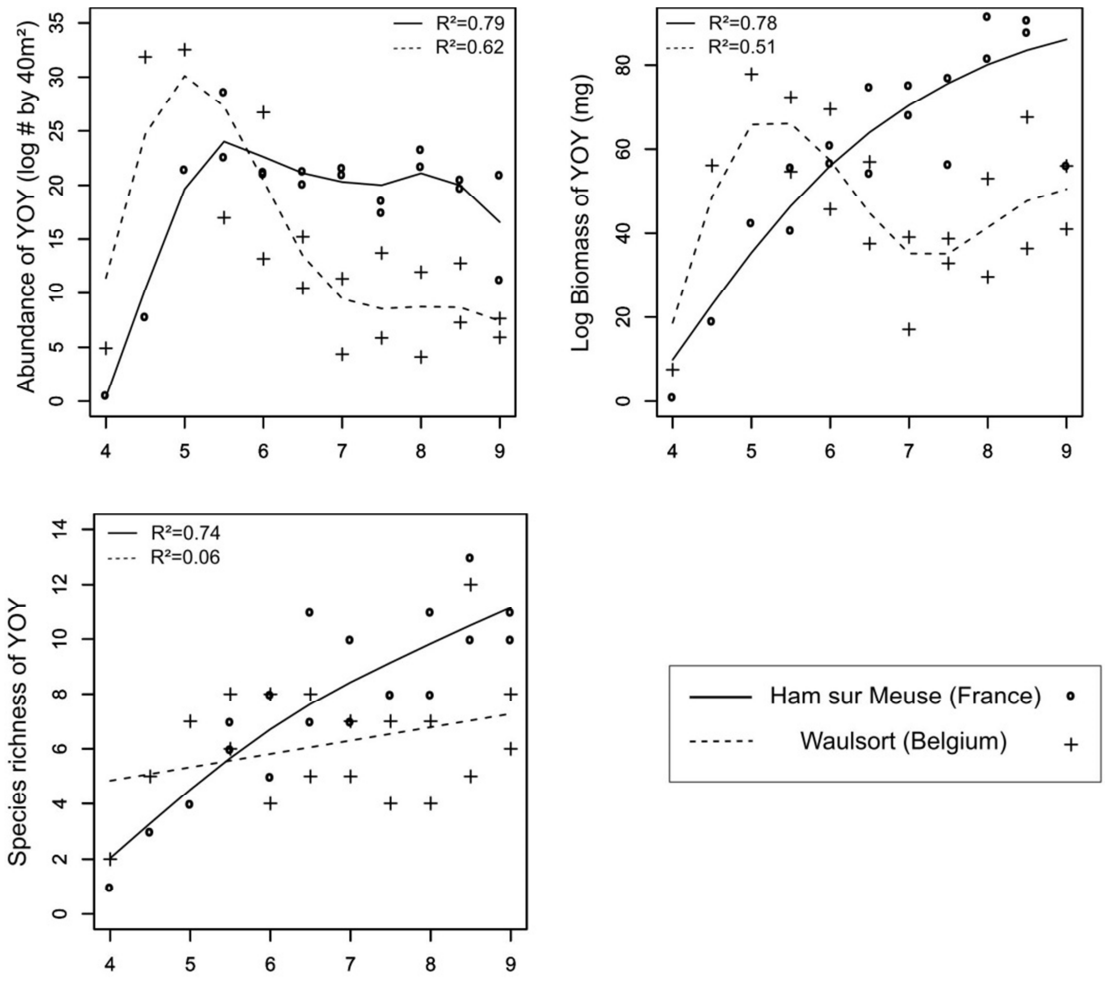
Temporal trends of population indices (abundance, biomass and specific diversity) were examined over the study period using Generalized Additive Models (GAM; Fewster, Buckland, Siriwardena, Baillie, & Wilson, 2000) and modelled as a smooth nonlinear function of time. Autocorrelation error was reduced by adding a residual autocorrelation structure, optimized by minimizing the AIC criterion over several combinations of autoregressive parameters (Zuur *et al.*, 2009).

With a Generalized Linear Model (GLM), we characterized the relation between population indexes with time and site interaction. We also used a GLM to identify relations between isotopic indices (SEA_C, Overlap, WIC/TNW) and the ontogenic stage, the species and the site. We realized the pairwise comparisons based on the Bonferroni adjustement with the *lsmeans* package (Lenth, 2016).

Normality of data and residuals were analysed with a Shapiro-Wilk test (Shapiro & Wilk, 1965)

Results

In both studied sites, we first caught larvae with a resorbed yolk sac from April (Figure 2), with a maximum reached in May (18.5 larvae by m²). After this date, the total abundance of YOY communities varied depending on the site (p = 0 .002, Table 2). In the most channelized site, YOY abundance strongly decreased while it remained constant until September at the less channelized station. The biomass and the species richness were significantly higher at Ham-sur-Meuse than at Waulsort, where they remained constant after a brief increase during the first months of the study (respectively p < 0 .001 and p = 0.005). Larval mortality of the earliest spawning species was potentially offset by the hatching of later breeding taxa at Ham-sur-Meuse, but not at Waulsort. The abundance of chub and roach varied in a similar way over time at both stations studied, with a rapid increase followed by a steady decrease. On the other hand, the abundance of the two other species differed according to the station: common bleak increased at Ham-sur-Meuse but not at Waulsort (p < 0 .001), whereas the contrary was observed for the European perch (p < 0.001).



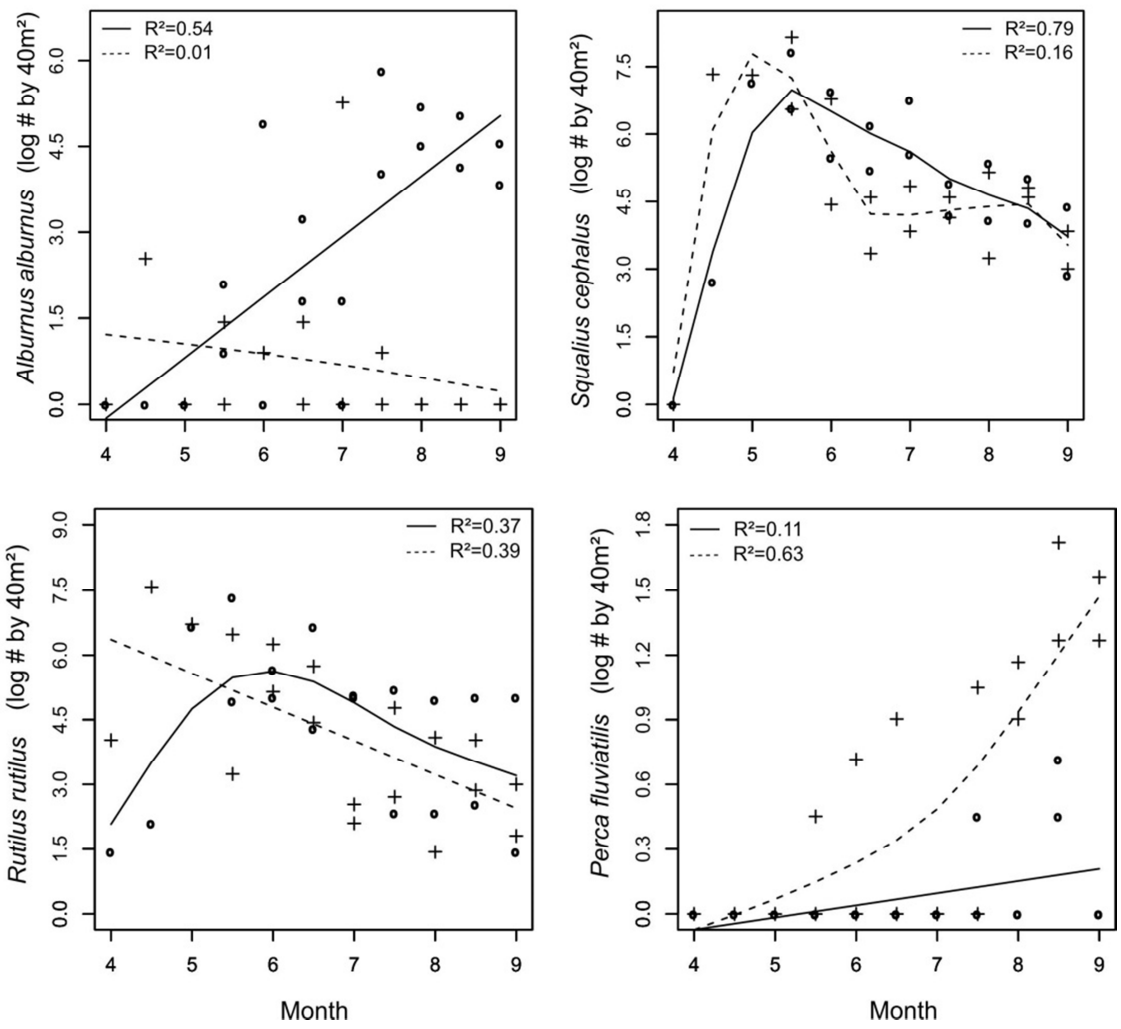


Figure 2: Temporal evolution of abundance, biomass and species richness of the YOY fish communities sampled at two sites of the Meuse River in 2013 and 2014. Abundances over time are shown separately for common bleak, chub, roach and European perch YOY. Temporal trends were modelled using Generalized Additive Models with residual autocorrelation structure. Solid line and dots corresponds to the lightly channelized reach and dashed line and crosses to the heavily channelized reach.

Table 2: Statistical evaluation of time and site effects with a generalized linear model for three population indices and YOY abundances of four species caught at two sites of the Meuse River (Ham-sur-Meuse in France and Waulsort in Belgium) in 2013 and 2014.

	***p*-values**		
	Site	Time	Site * Time
Abundance	0.054	**0.048**	**0.002**
Biomass	**0.005**	**0.001**	**< 0.001**
Species richness	**0.015**	**< 0.001**	**0.005**
Alburnus alburnus	**< 0.001**	**0.008**	**< 0.001**
Squalius cephalus	0.68	0.237	0.477
Rutilus rutilus	0.689	**0.013**	0.099
Perca fluviatilis	**< 0.001**	**< 0.001**	**< 0.001**

The diet of consumers for all stages of development was estimated with MixSIAR models (see Appendices 12, 13 and 14 for more details) for both sites. Benthic macroinvertebrates resources composed most of the diets of the four fish species (Figure 3). Planktonic resources and terrestrial vegetation were minimal components of larvae, juveniles or adults' diets at both sites. During the early ontogenic stages, fish assimilated a larger part of aquatic vegetation, mainly algae (95% Credibility Interval (CI): 5-57%), which tended to decrease as fish grew (95% CI: 2-45%) in favor of fish prey, notably at Waulsort (95% CI: 9-74%). At Ham-sur-Meuse, fish had a modelled diet mostly consisting of macroinvertebrates whereas at Waulsort, fish consumed larger quantities of aquatic vegetation and YOY (Figure 3). However, the contribution of small YOY for larvae and juveniles was smaller for cyprinids than for juvenile European perch and for adults (except bleak).

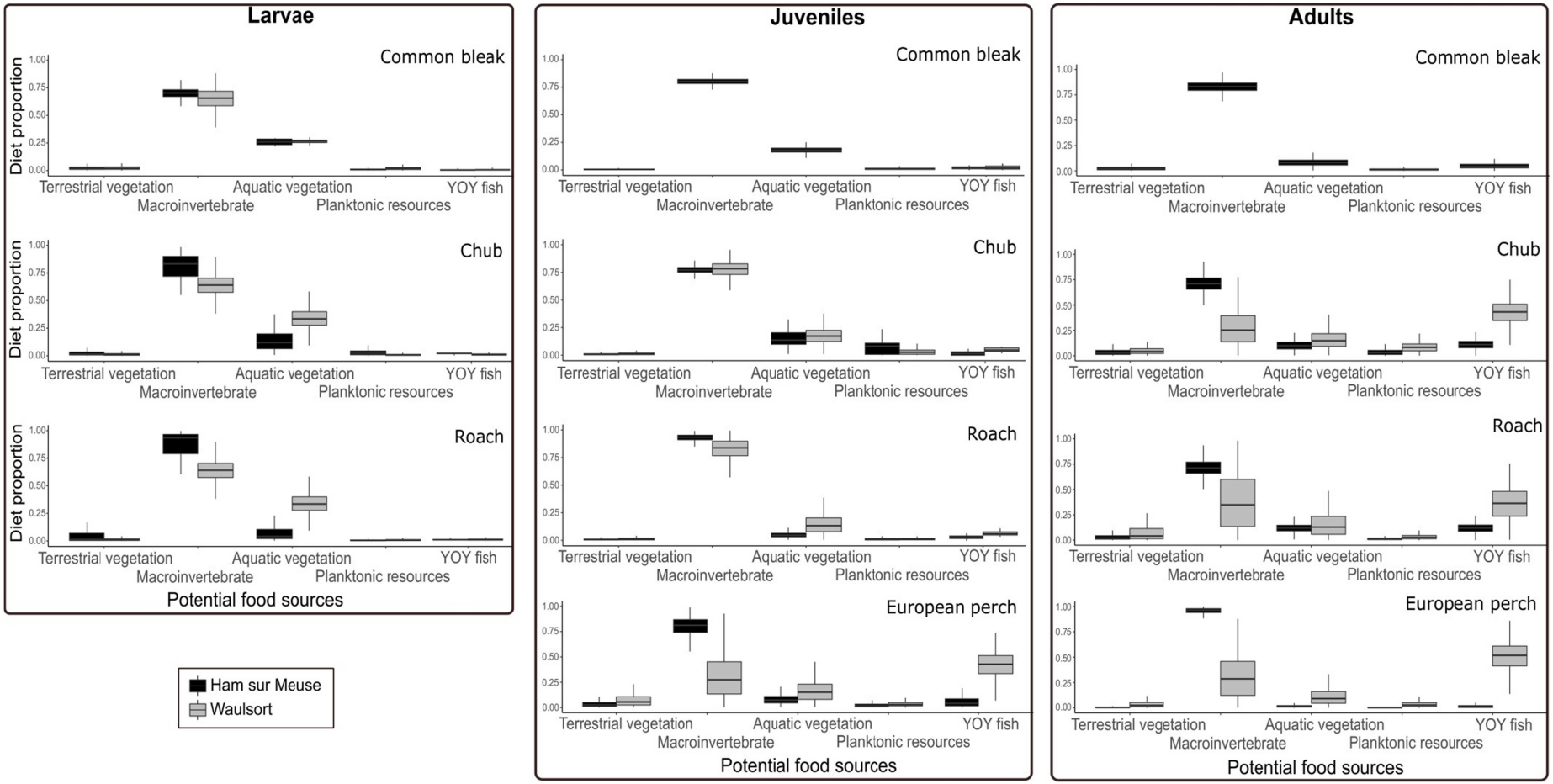


Figure 3: Diet composition, as depicted by the MixSIAR model, of 4 species of fish at 3 ontogenic stages, based on the individual $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values and the potential food sources sampled at Waulsort and Ham-sur-Meuse between 2013 and 2014 (see Appendix 12 for details). Median: lines in center of boxes, 50% Credibility Interval (CI): box boundaries, 95% CI: error bars.

The isotopic niche areas (SEA_C) and the niche overlaps of the twelve groups (4 species and 3 stages) modelled with SIBER (see Appendix 15 for more details) did not differ between the studied sites, and the slopes of the regression between these two parameters were not significantly different, reflecting an absence of interaction with sites (p = 0 .8, Figure 4).

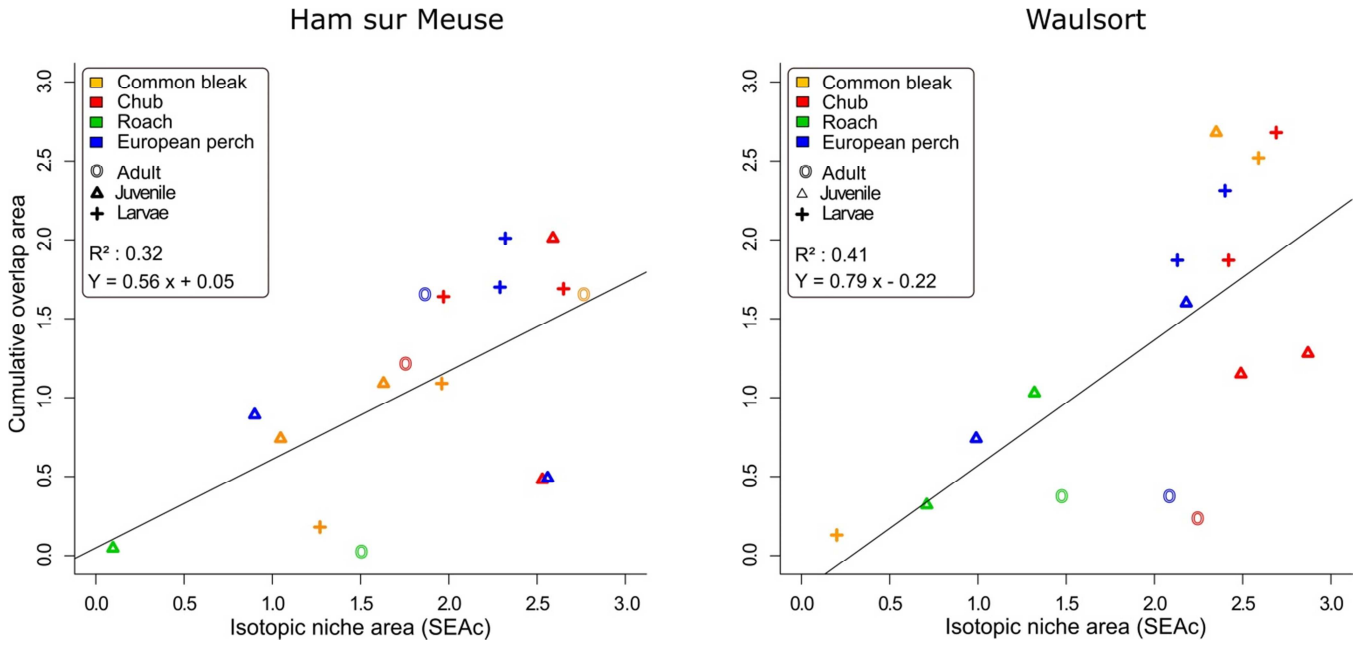


Figure 4: Relationship between the isotopic niche area (SEA_C) and the cumulative overlap area between isotopic niches of 4 species of fish captured on 2 sites of the Meuse River differing by the degree of regulation, in 2013 and 2014.

This finding is confirmed by a post-hoc test (Figure 5) which highlights that the isotopic niche overlaps between species were significantly wider during the early-life stage (larvae, $p <$ 0 .001) while the isotopic niche size (SEA_C) did not significantly differ (Figure 5). In both sites, niche overlap was greater during the larval stage.

At each ontogenic stage, the three species of cyprinid fish (common bleak, chub and roach) had a niche overlap significantly higher than European perch ($p <$ 0 .01), and two of the cyprinids depended on a greater diversity of resources than the perch (larger SEAc for chub, $p <$ 0 .01, and roach, $p <$ 0 .05).

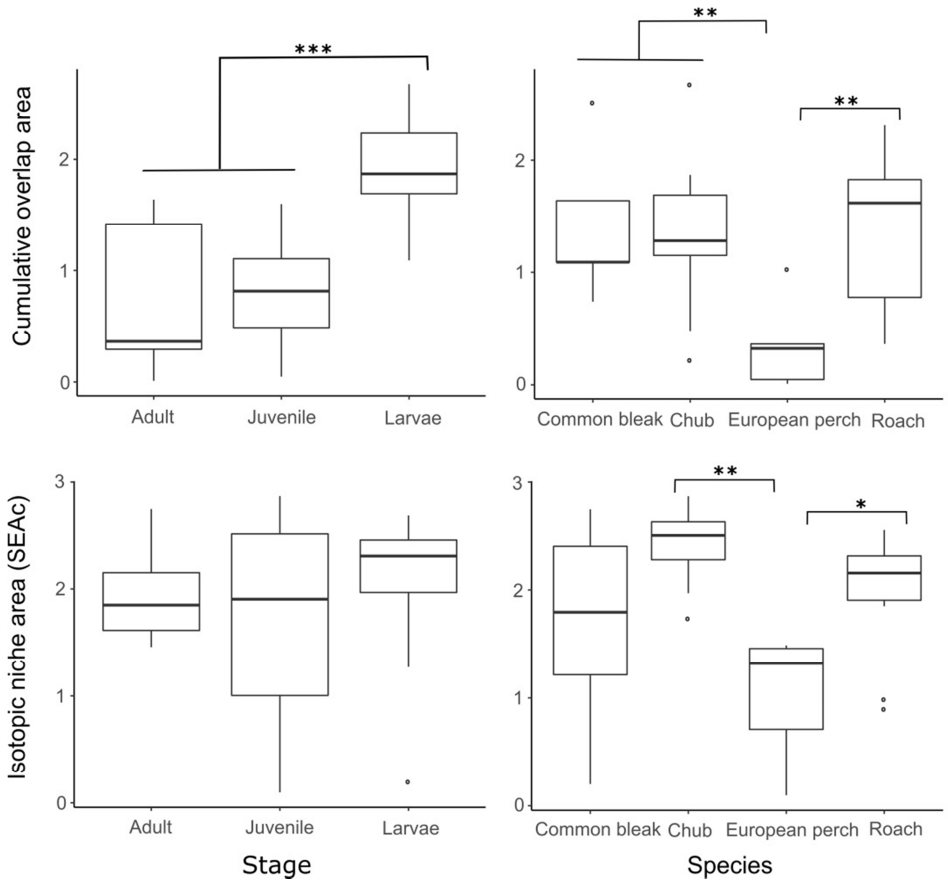


Figure 5: Comparison of the isotopic niche area (SEA_C) and the cumulative overlap area between isotopic niches of 4 species of fish captured on 2 sites in 2013 and 2014. The significance of the interaction was tested using a generalized linear model (* P < 0.05, ** P < 0.01, *** P < 0.001).

By studying the diet of each individual (WIC) related to the group to which it belongs (TNW) we evaluated the relative degree of individual specialization (individuality). The slope of the regression was significantly different between the two sites ($p < 0.001$) which suggests that at least one studied group had a more specialized diet at Waulsort than at Ham-sur-Meuse (Figure 6). Individual specialization appeared higher (and WIC lower) relative to total niche variation (TNW) at Waulsort, indicating that some specimens consumed prey which strongly differed from the rest of the population in the most channelized reach.

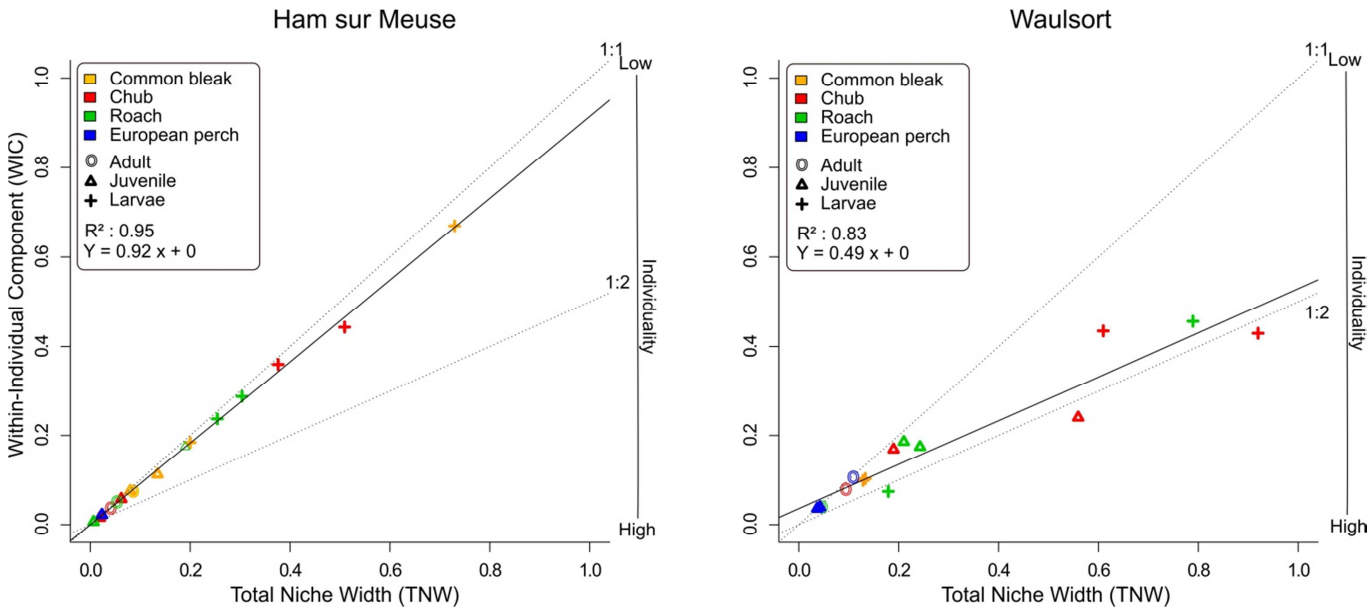


Figure 6: Relationship between the Total isotopic Niche Width (TNW) and the Within-Individual Component (WIC) of 4 species of fish captured on 2 sites of the Meuse River by the degree of regulation during 2013 and 2014. The slope of the relationship (solid lines) is an indicator of the dietary specialization of the populations.

The post-hoc test established that larvae had a more specialized diet in the Belgian site than those of the French site ($p < 0.01$, Figure 7). Furthermore, roach larvae were more generalist at Ham-sur-Meuse ($p < 0.05$) than at Waulsort, and chub and bleak larvae tended to follow the same trend.

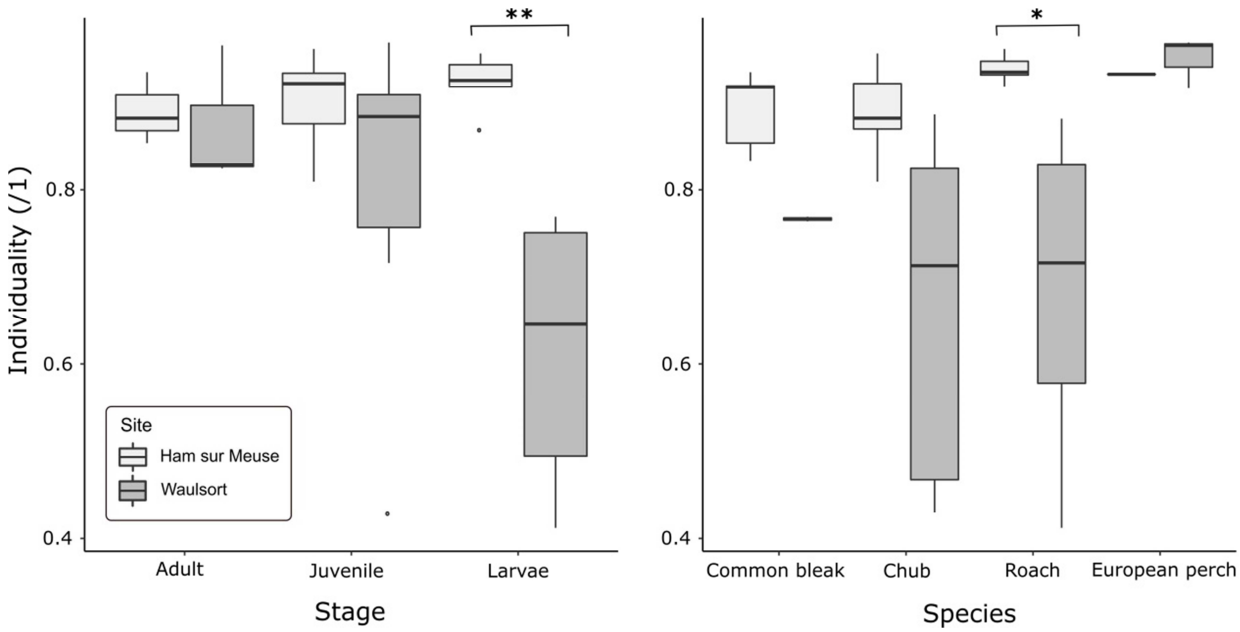


Figure 7: Comparison of dietary specialization (WIC/TNW) by life stage and species for four species of fish captured at two sites on the Meuse River in 2013 and 2014. Lower values indicate greater specialization. The significance of the relationship was tested using a generalized linear model (* P < 0.05, ** P < 0.01, *** P < 0.001).

Discussion

Ecological impacts of river regulation on habitat diversity and fish assemblages have been widely documented, but their role in the trophic competition between fish ontogenic stages has been poorly investigated so far (Mapes *et al.*, 2015; Wedderburn *et al.*, 2017). In a low planktonic resource context, we hypothesized that the habitat heterogeneity potentially offers a greater resource availability and diversity, which increases the abundance of young of the year fish and reduces trophic competition, notably during the earlier stages of development.

Our observations supported the hypothesis that river regulation potentially influences fish recruitment. Between April and June, abundance of YOY increased in a similar way at both sites. However, in the channelized reach, YOY abundance decreased afterwards, whereas it remained constant in the less regulated reach. This may be related to the later reproduction of other fish species as tench *Tinca tinca*, common carp *Cyprinus carpio*, minnow *Phoxinus phoxinus*, barbel *Barbus barbus* or common bream *Abramis brama*, which compensated mortality of the early spawning species as roach and chub (Bass, Pinder, & Leach, 1997; Pinder, 2001). The habitat diversity due to lateral connection and low-regulated main stream could improve fish recruitment by offering nursery habitat for a larger number of species, and potentially a wider diversity of food sources (Schiemer, Spindler, Wintersberger, Schneider, & Chovanec, 1991; Keckeis, Winkler, Flore, Reckendorfer, & Schiemer, 1997; Reckendorder *et al.*, 2001; Konrad *et al.*, 2016; Nagayama & Nakamura, 2018). In the Ouse River, the recruitment of numerous species decreased and many cyprinid fish became locally extinct due to the river regulation and habitat homogenization (Copp, 1997). In the Maumee River, lithophilic spawning fish and many cyprinid larvae benefited from the improvement of habitat quality and complexity (Mapes *et al.*, 2015). In this study, habitat diversity did not impact the recruitment of the two generalist species, roach and chub, whose density was comparable to other rivers (Valová *et al.*, 2006). This is in agreement with the report by Jurajda, Reichard, Hohausová, & Černý (2001) on rivers of the Danube basin, where river channelization barely impacted limnophilic species. In contrast, rheophilic species as nase *Chondrostoma nasus* or spirlin bleak *Alburnoides bipunctatus* were more sensitive to river flow regulation, with the exception of chub which was potentially better adapted to hydro-morphological modifications (Valová *et al.*, 2006).

The abundance of common bleak and European perch YOY differed in the Meuse River according to the studied reach. This divergence could be linked with the density of adult European perch which decreased over time in the French site, but remained constant in the Belgian section, while the opposite was observed for the common bleak (Alonso *et al.*, 2014; Benitez *et al.*, 2015). In another study, we showed that plankton decline and increased predation risk (*e.g.* the great cormorant *Phalacrocorax carbo* and the European wels *Silurus glanis*) influenced trophic structure of the fish community of the Meuse River (Latli *et al.*, 2017a), which could potentially differ according to the diet type and the importance of human perturbation.

The temporal changes in YOY catches could also be attributed to deliberate dispersal movements. During early stages, fish disperse from nursery areas to appropriate rearing habitats (Lechner *et al.*, 2016) mainly at night to reduce predation risk (Johnson & McKenna, 2007). This dispersion could occur accidentally, following high flow episodes for example (Pavlov *et al.*, 2008). The motivation of intentional drifting is not clearly addressed in the literature and may be stimulated by food availability or search for a specific habitat (Lechner *et al.*, 2016), but to our knowledge, there are no studies linking food quality or quantity to YOY drift events.

YOY fish are sensitive to environmental changes (Jurajda *et al.*, 2001; Wedderburn *et al.*, 2017) but also to food availability (Nunn, Harvey, & Cowx, 2007). In the Meuse River, the decrease of planktonic production has resulted in a diet shift of the four studied fish species, which turned to foraging in the benthos independently of the degree of channelization and the abundance of riparian resources (Latli *et al.*, 2018). Our results show that the diet of different cyprinid larvae and juveniles was mainly composed of benthic macroinvertebrates, with minor contributions of aquatic vegetation. YOY shift to benthic prey when planktonic prey decrease, which could indicate that benthic invertebrates were their optimal food sources in a low planktonic context (Nunn *et al.*, 2012). A similar response has been reported by Hoogenboezem, Lammens, van Vugt, & Osse, (1992) for the common bream under zooplankton abundance lower than 500 ind.L^{-1}. For many cyprinids and percids, switching from water column feeding to a selective capture of benthic prey could decrease the relative energy gain (Nunn *et al.*, 2012) and enhance competition, which could be mitigated by habitat diversity and presence of alternative resources (Pintar & Resetarits, 2017).

YOY fish diet was partly composed by aquatic vegetation (*i.e.* bryophytes, spermaphytes, algae…) which could be important for some species (e.g., 25-29% of the larval diet for common bleak). This low-energy food contributed more to YOY fish diet in the more heavily channelized reach, while macroinvertebrates were preferred in the other one. Adult diet also differed according to the studied site. In the less channelized reach, the diet of the four species comprised mostly benthic macroinvertebrates, while, in the other site, macroinvertebrates were less consumed and feeding on aquatic vegetation and on small fish contributed more to adult diets. At Waulsort, almost half of the diet of European perch, chub and roach was composed by YOY fish, while at Ham-sur-Meuse this proportion was less than 20% even for the European perch, which is known to prey upon fish larvae in addition to macroinvertebrates (Linzmaier *et al.*, 2018). Fish feeding habits at Waulsort could be linked with lower availability of benthic macroinvertebrates, and with higher competition for food between consumers. The poor habitat structural complexity could also have facilitated predation on YOY fish at Waulsort, by increasing the foraging success of multiple predator species (Warfe & Barmuta, 2004). Therefore, YOY were potentially affected by both low food availability and high predation risk.

In the absence of planktonic resources, YOY cyprinids mostly consumed the same resources whatever their ontogenic stages (i.e. larval or juvenile). Theoretically, when resource

availability is reduced, fish trophic niche width tends to increase due to the diminution of their preferred diet (Bison *et al.*, 2015). Juvenile fish generally consumed a broader range of prey types (zooplankton, macroinvertebrate larvae…) than larvae. Older YOY likely easily feed on a wide range of preys due to a larger mouth size and improved mobility (Nunn *et al.*, 2012). However, we found that trophic niche areas of the two ontogenic stages studied were similar regardless of the site. Niche overlap, on the other hand, was higher for larvae. This provides some evidence that the plankton diminution reduced the larval diet diversity, causing them to forage on other resources, such as benthic macroinvertebrates which are also coveted by juveniles (Nunn *et al.*, 2007a). Larvae were potentially constrained towards greater herbivory, which could have been less metabolically efficient and might have decreased growth rates (Post & Parkinson, 2001).

Trophic competition and predation risk promoted diet plasticity, which could impact less competitive species such as common bleak (Lammens & Hoogenboezem, 1991). In the Meuse River, YOY and adult abundance of common bleak decreased since the 1990s in the heavily channelized reach (Benitez *et al.*, 2015), potentially due to the increase of great cormorant abundance and the decrease of planktonic resources (Latli *et al.*, 2017a). Conversely, the low plankton availability recorded in the Meuse River affected the trophic niche of the European perch in Waulsort differently. Contrary to YOY cyprinids, perch juveniles had a smaller isotopic niche which means that they consumed less diverse resources; they mainly focused on benthic macroinvertebrates and YOY fish prey. Furthermore, European perch seemed less affected by the interspecific competition, as their niche overlap was smaller than the one of cyprinids. Due to an early hatching and a rapid growth (Pinder, 2001), young perches could swallow fish larvae and large benthic macroinvertebrates potentially inaccessible to other YOY taxa (Persson & Hansson, 1999).

Even though food depletion could increase mortality, it is rarely observed because food competition generally favors diet partition between consumers (Olsson *et al.*, 2006). Moreover, intensification of trophic competition does not necessarily entail any effect on the population niche, but can instead promote diet diversification within a population, i.e. individual specialization (Araújo *et al.*, 2011; Bolnick *et al.*, 2010). Here, larval isotopic niche widths (a proxy of the diversity of resources used by a population) were similar between sites. However, channelization induces individual trophic specialization of larvae. In the less regulated reach, cyprinid larvae had a generalist diet, while in the heavily channelized reach individuals exhibited a more specialized diet oriented towards several macroinvertebrate taxa or aquatic vegetation. Many authors reported that individual specialization is a way to reduce trophic competition (Araújo *et al.*, 2011; Dias *et al.*, 2017). In the channelized reach of the Meuse River, larval specialization seems to be a way to deal with plankton rarefaction and increased trophic competition for macroinvertebrates with older stages of fish. Despite the fact that abundance of YOY cyprinids was similar in the two sites, all larvae from Ham-sur-Meuse focused on their optimal source food, i.e. a large panel of macroinvertebrate taxa. At Waulsort, low habitat diversity likely increased the resource partitioning between YOY

(Marklund *et al.*, 2018) and forced the less competitive stages (*i.e.* larvae) to consume less energetic food sources as bryophytes and algae.

Early life stages are critical periods for many organisms, and they require more accurate study to improve our understanding of community ecology and ecosystem functioning in a framework of human disturbances (Mapes *et al.*, 2015). This study highlights the key role of intraspecific resource repartition for YOY fish having to cope with plankton-depleted conditions. Younger cyprinid stages seem more affected by intra and interspecific competition in the more channelized reach. YOY fish communities were also less diversified and abundant in the more altered site, which highlight the importance of limiting channelization for a better fish community conservation.

Ce qu’il faut retenir de ce chapitre

Dans le 6ème chapitre, nous nous intéressons à la compétition alimentaire de 4 espèces de poissons aux stades alevin, juvénile et adulte dans deux biefs de la Meuse différements aménagés. Nous émettons l’hypothèse qu’en cas de faible disponibilité des ressources planctoniques, la compétition alimentaire est plus importante pour les jeunes stades au niveau de la station la plus anthropisée, réduisant leur aptitude à atteindre l’âge adulte.

L’abondance des alevins diminue au cours du temps dans la station aménagée tandis qu’elle reste relativement constante au niveau de la station moins impactée. La diversité de l’habitat permet potentiellement la reproduction et la croissance d’alevins de différentes espèces de poissons en Meuse française qui compense la mortalité naturelle des alevins nés au début du printemps.

Le régime alimentaire des poissons de la Meuse, en cas de faible disponibilité des ressources planctoniques, est composé majoritairement de macroinvertébrés benthiques et de végétaux aquatiques. Les alevins consomment une part plus importante de végétaux aquatiques que les juveniles, malgré le faible intérêt énergétique de cette ressource. Cet attrait pour les végétaux peut être expliqué par une exclusion alimentaire forcée par les juvéniles plus efficace que les larves dans la capture de proies de taille plus importante comme les macroinvertébrés.

La plus grande diversité des ressources alimentaires en Meuse française induit un régime alimentaire généraliste chez les alevins. Au contraire, en Meuse belge la plus faible diversité potentielle des ressources ne permet pas aux alevins de limiter la compétition trophique ce qui peut créer une spécialisation alimentaire chez les plus jeunes stades forçant une partie des individus à consommer des ressources peu énergétiques.

Chapitre 7

Discussion générale

1. Etat des lieux de la Meuse: tendances temporelles hydrologiques et hydrobiologiques d'un fleuve anthropisé

A bien des égards, la rivière Meuse semble être un écosystème particulièrement dégradé à l'échelle locale, du fait des activités anthropiques et de la densité de population particulièrement importante localisée sur une grande partie de son bassin versant. De plus, à l'instar des grands cours d'eau de la planète, la Meuse souffre d'atteintes plus globales liées aux phénomènes de changement climatique et d'invasions biologiques. Etudier l'évolution temporelle des variables thermiques, hydrauliques, physico-chimiques ou biologiques d'un grand cours d'eau requiert un suivi à long terme couvrant un long linéaire de la rivière. Basé sur un suivi couvrant un linéaire de 427 km de rivière (5 sites) pendant 24 années (1987-2011), nous avons pu mettre en évidence que depuis la fin des années 80, la moyenne de la température annuelle de l'eau a progressivement augmenté (de l'ordre de 0,9°C). Ce changement graduel, corrélé aux températures de l'air, est comparable à ce qui est reporté par d'autres scientifiques aux Etats-Unis (augmentation des températures de 0,009 à 0,077°C par an selon Kaushal *et al.*, 2010). Toutefois, cette augmentation de la température de l'eau ne s'accompagne pas d'une diminution des débits comme constaté au niveau de rivières plus méridionales comme la Loire où, au cours des 3 dernières décennies, le débit moyen a diminué d'environ 25% (Floury *et al.*, 2012). La concomitance de ces deux paramètres affecte particulièrement les macroinvertébrés benthiques de la Loire notamment au cours de la période estivale. Les taxons rhéophiles à tendance psychrophile, comme les Chloroperlidae, Perlodidae et les Oligoneuriidae, ont été rapidement affectés par le réchauffement des eaux (Floury *et al.*, 2013). Les macroinvertébrés benthiques de la Meuse ne présentent pas la même réponse aux changements climatiques, seule l'abondance des taxons définis comme eurythermes répond significativement à l'augmentation de la température de l'eau. Il faut toutefois tempérer ce résultat car la base de données utilisée pour cette étude ne permet pas de répondre objectivement à cette question. Premièrement, la chronologie de données exploitables des inventaires de macroinvertébrés est assez courte et débute en 1998. A cette période, il est probable que les taxons les plus sensibles aient déjà disparu des stations étudiées du fait du développement de l'eutrophisation. En effet, l'impact du réchauffement des eaux pourrait être confondu par le niveau de pollution organique, particulièrement important au cours de la période 1970-1980, spécialement au niveau des stations les plus en aval avec des teneurs moyennes annuelles en ammonium maximal de 2,7 mg N/L et en orthophosphates de 0,8 mg P/L. Deuxièmement, les analyses ont été réalisées sur des inventaires annuels et nous aurions obtenu une meilleure précision en incorporant l'aspect saisonnier dans nos calculs. Néanmoins, l'impact du réchauffement sur la biocénose des rivières ne doit pas être minimisé car il peut avoir une incidence indirecte sur l'écosystème, en amplifiant l'effet des

toxiques, en favorisant l'implantation d'espèces exogènes ou en provoquant une hausse de la productivité du système (Caissie, 2006; Johnson *et al.*, 2009).

La hausse de l'état trophique induite par le réchauffement des eaux (Jennings *et al.*, 2009) n'a pas été constatée en Meuse mais, à l'inverse, les concentrations de phytoplancton et de zooplancton ont fortement diminué (plus de 85%) sur la période étudiée. Bien que l'épuration des eaux ait réduit significativement les apports anthropiques de nutriments dans la rivière, les concentrations en phosphate et en azote restent non limitantes au développement du phytoplancton contrairement à d'autres rivières européennes comme la Loire (Larroudé *et al.*, 2013; Minaudo *et al.*, 2015). Le déclin des populations planctoniques de la Meuse est attribué aux mollusques invasifs filtreurs, Corbiculidae et Dreissenidae (Pigneur *et al.*, 2014), qui par leur densité importante et leur plasticité phénotypique sont capables de s'adapter et de modifier différents écosystèmes (Strayer *et al.*, 1999). On retrouve ces organismes dans de nombreux hydrosystèmes de France [*e.g.* Rhône (Daufresne *et al.*, 2007)], d'Europe [*e.g.* Grande Bretagne (Bowes *et al.*, 2011)], du monde [*e.g.* rivière Hudson (Strayer *et al.*, 2008), río de la Plata (Lercari & Bergamino, 2011)].

De nombreuses observations, compilées par Gallardo *et al.* (2016), reportent que l'invasion de mollusques filtreurs influence négativement les populations planctoniques mais a un effet positif sur les communautés de macroinvertébrés benthiques et aucun impact vis-à-vis de la faune ichtyologique. La plupart de ces études ne sont basées que sur des indices écologiques relativement globaux (abondance, diversité et équitabilité) et ne sont pas assez précis pour déceler les perturbations qui ont lieu au sein de la structure du peuplement. Dans notre étude, aucune tendance globale nette n'est ressortie de l'utilisation des indices plus généraux hormis l'augmentation de la diversité taxonomique des macroinvertébrés probablement liée à l'apparition de nouvelles espèces exogènes. En revanche, l'utilisation des traits d'histoire de vie a permis de discerner les modifications fonctionnelles induites par la réduction du phytoplancton sur les communautés. Les réponses biologiques d'ordre trophique corrélées à la raréfaction des ressources planctoniques sont les plus notables. Tout d'abord, la structure trophique des communautés ichtyologiques a évolué, l'abondance des poissons omnivores se nourrissant dans la colonne d'eau (ablette commune, gardon…) a significativement diminué. En revanche, la proportion d'espèces benthiques consommant des macroinvertébrés a largement progressé. Certaines espèces de poissons partiellement planctonophages ou passant par ce stade durant les premiers mois de leur développement (Thorp & Casper, 2003) ont certainement été pénalisées par la diminution du plancton et plus spécialement des rotifères. Les rotifères dominaient les communautés planctoniques durant les années 90 mais restent particulièrement sensibles à la prédation des mollusques invasifs (Jack & Thorp, 2000). Ce sont, en outre, les proies préférées de nombreuses larves de poissons (Nunn *et al.*, 2007a). La structure trophique des macroinvertébrés benthiques a également été affectée par la diminution du plancton mais de manière différente de celle des poissons. La réduction de la turbidité a permis une plus grande pénétration de la lumière favorisant le développement du periphyton et des organismes brouteurs (scrapers) profitant de cette manne alimentaire.

Les changements structurels directs des communautés de macroinvertébrés benthiques liés à la diminution du plancton sont relativement peu importants, toutefois des conséquences indirectes semblent avoir une plus forte incidence. L'accroissement du nombre d'invertivores exerce une pression sérieuse sur les macroinvertébrés à tel point que la structure des communautés évolue conjointement avec le risque de prédation. Les taxons favorisés disposent des traits d'histoire de vie que l'on attribue généralement aux espèces à stratégie « r » majoritairement de petite taille, à la croissance rapide, investissant énormément d'énergie à la reproduction et à la dispersion des gamètes (Pianka, 1970). Au contraire, les taxons à stratégie « K » qui ont une croissance ainsi qu'une maturité plus tardive, sont également plus sensibles aux perturbations environnementales. La proportion de ces individus répondant à ces caractéristiques décroît significativement dans les communautés de macroinvertébrés mais également de poissons de la Meuse. La pression de prédation exercée par le Grand cormoran peut être considérée pour les communautés ichtyologiques comme une perturbation limitant l'accès à certaines ressources ou réduisant le recrutement des espèces à maturité tardive (Orpwood *et al.*, 2010; Bergamino *et al.*, 2012).

L'évolution structurelle des communautés observées en Meuse est analogue aux observations ou prévisions rapportées sur d'autres cours d'eau du monde entier pour les macroinvertébrés (Durance & Ormerod, 2009; Floury *et al.*, 2013) et les poissons (Daufresne & Boët, 2007; Buisson & Grenouillet, 2009). La majorité des évolutions biologiques relatées, notamment celles liées aux stratégies r/K, est corrélée aux changements hydro-climatiques. Certains chercheurs suggèrent alors qu'il existe un patron de réponses biologiques à grande échelle des communautés aquatiques au réchauffement global (Floury *et al.*, 2013). Les changements structuraux observés en Meuse ne sont toutefois pas corrélés aux mêmes variations environnementales et je souhaiterais formuler deux objections tempérant l'hypothèse précédemment citée. Premièrement, la plupart des études mentionnées rapportent la colonisation du milieu par un ou plusieurs mollusques invasifs filtreurs ainsi qu'une réduction du phytoplancton. Toutefois, aucune étude n'a pris en compte l'influence indirecte de la réduction des ressources induisant l'accroissement du risque de prédation sur les taxons spécialistes plus sensibles, effet particulièrement important sur la Meuse. Deuxièmement, il est possible que le succès des taxons à stratégie « r » provienne en grande partie de l'abondance des espèces exogènes. Les taxons invasifs ont généralement une stratégie de propagation rapide basée sur une forte dispersion des gamètes et un cycle de vie relativement court. De plus, dans les grands fleuves anthropisés, ils représentent généralement une grande proportion des individus rencontrés, comme sur la Meuse belge où moins de 50% des macroinvertébrés benthiques capturés sont endogènes. Il faut néanmoins modérer ce résultat, car l'évolution des traits d'histoire de vie des poissons considérés dans cette étude suit la même tendance que les macroinvertébrés malgré la faible présence de taxons exogènes composant la communauté ichtyologique.

Malgré la concomitance des tendances biologiques observées, la divergence des causes suspectées entre les études illustre bien le contexte multi-stress dans lesquels évoluent les organismes des grands hydrosystèmes fluviaux et la difficulté d'identifier les relations

causales nettes. L'enchevêtrement des pressions peut nous amener à confondre différents effets rendant alors nos affirmations inexactes. Néanmoins, la diminution des ressources planctoniques induit des réponses biologiques fortes sur un long linéaire de la Meuse. Ces réponses semblent toutefois varier en fonction de la méthode de gestion du cours d'eau employée.

2. La diversité de l'habitat, un rempart face aux perturbations trophiques ?

Habitat et diversité trophique

Les communautés animales et végétales tendent à être peu diversifiées et abondantes dans les écosystèmes anthropisés du fait de l'homogénéisation ou de la fragmentation de l'habitat (Boët *et al.*, 1999). Cette affirmation parait éculée tant elle a été observée dans un grand nombre de milieux et rabâchée par les scientifiques (Riseng *et al.*, 2004). Le fleuve Meuse ne déroge pas à la règle et, bien que la diminution des ressources trophiques ait impacté les communautés sur un long linéaire indépendamment de sa qualité hydromorphologique, il apparaîtrait que certains taxons aient été plus affectés au niveau de la partie belge de la rivière. Il a été effectivement rapporté dans le chapitre 3 que les stocks de gardons et potentiellement d'ablettes communes ont décru de plus de 90% sur la période étudiée, suite à la diminution des ressources planctoniques et de l'augmentation du risque de prédation (Otjacques *et al.*, 2016). Cependant, une telle décroissance des populations de gardons n'a pas été observée par Alonso *et al.*, (2014) sur la partie non navigable de la Meuse française malgré le fait que le site étudié soit assujetti aux mêmes types de pressions qu'en Meuse belge (Latli *et al.*, 2017a). De plus, il semblerait même que l'abondance des taxons spécialistes, plus sensibles à la qualité de l'habitat et de l'eau, augmente à partir des années 2000 en Meuse française. Cette tendance, également observée sur la Loire (Floury, 2013), est probablement liée à l'amélioration générale de la qualité de l'eau de la Meuse, notamment de la diminution des matières organiques, confondant l'effet lié aux perturbations trophiques et biologiques décrites précédemment.

Certaines conséquences de la réduction des ressources planctoniques sur les communautés animales paraissent donc différentes en fonction de la qualité hydromorphologique de la rivière. Deux hypothèses pourraient expliquer cette divergence. La première concerne les fonctionnalités écologiques dépendantes de la qualité de l'habitat. Les espèces spécialistes requièrent un habitat diversifié et de qualité afin de satisfaire les différentes étapes de leur cycle biologique (McPeek, 1996). Par exemple, les radiers assurent le bon développement embryonnaire des espèces de poissons rhéophiles et les annexes hydrauliques forment un refuge adapté aux jeunes individus lors des variations hydrauliques (Copp, 1989). La communauté de macroinvertébrés benthiques est également très sensible à la qualité de l'habitat. L'hétérogénéité de l'habitat est généralement associée à une diversité taxonomique et fonctionnelle élevée (Wallace & Webster, 1996).

La seconde hypothèse qui pourrait expliquer le maintien des populations de gardons et autres espèces à tendance planctonivore en Meuse française malgré la diminution de cette ressource,

est la présence de sources alimentaires alternatives disponibles au sein des différents habitats recensés. La faible profondeur de la Meuse française associée à la présence de zones de rapides et de mouilles assure le bon développement de la végétation aquatique et du periphyton. Ces ressources pourraient compenser l'absence de matière nutritive dans le seston et ainsi maintenir les effectifs de certains taxons. C'est essentiellement cette hypothèse qui va nous préoccuper dans cette seconde partie de la discussion. Afin d'étayer notre argumentation, nous nous appuierons sur l'étude du régime alimentaire potentiel et observé des communautés de macroinvertébrés benthiques et de poissons de la Meuse belge et française.

Les macroinvertébrés constituent un maillon essentiel des réseaux trophiques aquatiques. Ils assurent le lien entre les producteurs primaires et les consommateurs secondaires ou tertiaires. Ils jouent également un rôle primordial dans la transformation des matières organiques autochtones et allochtones (Angradi, 1994). L'étude de la niche trophique potentielle des macroinvertébrés tend à confirmer qu'un habitat varié permet à la communauté de diversifier les sources alimentaires consommées. Bien que la diversité taxonomique soit plus élevée en Meuse belge, la répartition de l'utilisation des traits liés au régime alimentaire augmente au cours du temps en France mais non en Belgique. Ce résultat sous-entend que, suite à la diminution du plancton, les ressources consommées par la communauté de la Meuse française de macroinvertébrés sont mieux réparties qu'en Belgique. De plus, on y retrouve une part plus abondante d'individus présentés comme spécialistes, c'est-à-dire ayant un régime alimentaire théorique original vis-à-vis de l'ensemble de la communauté. Un habitat diversifié offrirait donc des ressources alternatives exploitables par les macroinvertébrés et limiterait l'impact de la raréfaction d'un type d'aliment. Ce résultat théorique, car il résulte d'une étude basée sur la niche potentielle de la communauté, est confirmé par l'étude isotopique de la niche trophique réalisée. La largeur de la niche trophique de la communauté de macroinvertébrés de France est plus importante qu'en Belgique ce qui indique que le régime alimentaire y est plus diversifié et composé partiellement de ressources ayant des valeurs de $\delta^{13}C$ plus proches de zéro, comme le périphyton et certains végétaux aquatiques (Perga, 2007).

Néanmoins, d'autres résultats tempèrent cette première affirmation. Premièrement, bien que les sources alimentaires soient plus variées dans le milieu moins perturbé, l'importance de la contribution des ressources autochtones comme les hydrophytes et le périphyton est visiblement accessoire pour la communauté de macroinvertébrés. Le régime alimentaire des macroinvertébrés des deux sites étudiés est majoritairement constitué de matières carbonées provenant de la végétation aquatique (algues et bryophytes) et de matières organiques détritiques issues essentiellement de la végétation riveraine. Des résultats analogues ont été publiés par de nombreux scientifiques (Angradi, 1994; Zeug & Winemiller, 2008; Thorp & Bowes, 2017) sur de grands fleuves américains. Comme pour la rivière Meuse, les apports algaux et des matières issues des plantes terrestres contribuent majoritairement à la biomasse de macroinvertébrés et de poissons. Il existerait néanmoins certaines variations liées à la dynamique hydrologique de la rivière. En période d'étiage, la contribution algale est majoritaire, et en cas de débit plus élevé ou de plus grande charge de sédiments en

suspension, l'apport des plantes terrestres dans le réseau trophique augmenterait (Roach *et al.*, 2015).

Deuxièmement, on observe une dissemblance importante des réponses trophiques des consommateurs en fonction du type de niche étudié (potentielle/observée). L'étude des traits liés à l'alimentation indique clairement une contribution théorique du périphyton très importante pour la communauté de macroinvertébrés composée de près de 25% d'individus brouteurs et un très faible apport des plantes aquatiques. Cette divergence pourrait être expliquée par un biais dû à l'inventaire des organismes. En effet, la modélisation isotopique de la communauté est constituée majoritairement d'individus collecteurs, de mangeurs de sédiments fins ou de broyeurs, capturés uniquement à l'aide d'un Surber. En revanche, les données employées afin de calculer la niche potentielle de la communauté de macroinvertébrés proviennent d'inventaires plus complets (IBGA) et affichent une proportion élevée de brouteurs. Il aurait idéalement été préférable d'utiliser les organismes obtenus via un inventaire biologique unique afin d'évaluer conjointement la niche trophique potentielle et observée (Devictor *et al.*, 2010). Il faut également garder à l'esprit que les macroinvertébrés affichent une plasticité importante du régime alimentaire qui évolue en fonction des stades larvaires ou de la taille des organismes (Usseglio-Polatera *et al.*, 2000), complexifiant ainsi la comparaison des méthodes.

Habitat et compétition alimentaire

De même que pour les macroinvertébrés, les communautés ichtyologiques ont également été affectées par la diminution trophique et le risque de prédation. Ces pressions ont restreint, au sein des deux sites, l'équilibre de l'utilisation des traits liés à l'alimentation, limitant l'abondance des poissons omnivores et piscivores au profit des insectivores. Néanmoins, la disponibilité des ressources planctoniques n'affecte pas directement les individus adultes, l'effet est plus insidieux sur les populations car il réduit principalement le succès du recrutement. Une étude de Cryer *et al.* (1986) témoigne de l'importance du zooplancton, notamment de l'abondance des rotifères et copépodes dans le succès du développement et donc, de la survie des larves de gardons en milieu lacustre. Lors des années où le pic de production du zooplancton correspond à l'éclosion des jeunes gardons, le recrutement des gardons est optimal. En cas de faible abondance de plancton, les alevins se tournent généralement vers divers types de proies plus ou moins efficients en terme de rapport énergétique tels que les végétaux aquatiques ou les macroinvertébrés benthiques (Nunn *et al.*, 2007a, 2012) renforçant la disparité des régimes alimentaires ainsi que la compétition trophique entre les individus (Welker *et al.*, 1994). Les rivières non navigables offrant une mosaïque d'habitats, donc de proies potentielles et de refuges, plus importante qu'en milieu aménagé pour la navigation, nous pouvons suspecter que la survie des larves y est supérieure et que la compétition alimentaire y est moins féroce.

L'évolution de l'abondance relative a été mesuré via des inventaires bimensuels recouvrant une période critique de la vie des jeunes poissons de l'année, depuis la résorption de la vésicule vitelline jusqu'à l'apparition de la plupart des caractéristiques d'adultes liées à la

mobilité. La comparaison de l'évolution de l'abondance des larves et des juvéniles entre les deux sites confirme les observations réalisées au chapitre précédent. L'abondance des alevins augmente exponentiellement durant les mois d'avril et de mai puis reste constant en Meuse française mais décroit sur le linéaire belge étudié. Cette différence peut être expliquée par l'évolution de la diversité taxonomique des alevins recensés qui augmente graduellement en France tandis qu'elle reste constante en Belgique. La station faiblement anthropisée permet donc à un plus grand nombre d'espèces de poissons, principalement des taxons plus exigeants en terme d'habitat, d'y réaliser l'entièreté de leur cycle biologique. La reproduction plus tardive des tanches, des vairons et des barbeaux fluviatiles (Pinder, 2001) compense la mortalité naturelle des espèces à éclosion plus précoce comme les gardons et les chevaines. La diversité de l'habitat aquatique et la présence d'annexes hydrauliques sont deux critères essentiels au maintien d'une communauté diversifiée car ils offrent des sites de reproduction pour les adultes mais également des zones de refuge et d'alimentation pour les alevins (Humphries & Lake, 2000; Konrad *et al.*, 2016; Nagayama & Nakamura, 2018). Dans la rivière Ouse, l'homogénéisation de l'habitat et la régularisation des débits a conduit à l'extinction locale des espèces les plus exigeantes (Copp, 1997). Dans la rivière Maumee, les travaux de diversification de l'habitat ont permis l'amélioration du recrutement des espèces cyprinicoles lithophiles (Mapes *et al.*, 2015). En revanche, Jurajda *et al.* (2001) ont observé dans le bassin du Danube que les espèces cyprinicoles généralistes sont peu impactées par la régulation des cours d'eau. De plus, contrairement à de nombreuses espèces rhéophiles, comme l'ablette spirlin ou le hotu, les chevaines sont peu sensibles aux modifications d'ordre hydro-morphologique (Valová *et al.*, 2006). Nos résultats sont en accord avec ces observations, aucune différence d'évolution de l'abondance des jeunes de l'année de gardons et de chevaines en fonction du degré d'anthropisation du cours d'eau n'a été constaté en Meuse.

Les jeunes poissons de l'année sont sensibles aux changements environnementaux (Jurajda *et al.*, 2001; Wedderburn *et al.*, 2017) mais également à la disponibilité des ressources (Nunn, Harvey, & Cowx, 2007). Faute de données antérieures à cette étude, il est impossible d'étudier les conséquences directes de la privation de zooplancton sur les alevins de la Meuse, mais il est envisageable d'extrapoler son effet sur les jeunes de l'année en fonction du degré d'aménagement de la rivière. Du fait que les larves de cyprinidés soient essentiellement planctonophages pendant les premiers mois de leur existence (Pekcan-Hekim *et al.*, 2016), la raréfaction de cette ressource a induit un *shift* alimentaire de ces larves indépendamment du degré d'aménagement du cours d'eau. Les larves ainsi que les juvéniles consomment majoritairement des macroinvertébrés benthiques mais également divers types de végétaux. De nouveau, le périphyton n'est que très peu consommé au contraire des algues filamenteuses et des bryophytes. Selon "l'optimal foraging theory" le passage d'un régime alimentaire centré sur le zooplancton vers des proies benthiques peut réduire le gain net énergétique (Nunn *et al.*, 2012), augmenter la compétition alimentaire et forcer les alevins à migrer vers de nouveaux habitats ou de nouvelles ressources (Pintar & Resetarits, 2017).

Le régime alimentaire des plus jeunes individus tend à être composé d'une part plus importante de végétaux aquatiques (jusqu'à 25-29% pour la larve d'ablette, IC à 95%) qui décroit avec le stade de développement. De plus, la proportion de végétaux consommés est généralement moindre pour la station peu aménagée. Ce résultat corroboré par l'étude des niches isotopiques et par la spécialisation individuelle au sein des différents stades ontogéniques permet d'identifier certaines interactions trophiques. Forcées par le manque de ressources planctoniques, les niches trophiques des alevins et des juvéniles sont partiellement superposées ce qui peut se traduire par l'assimilation des mêmes types de proies. Cependant, du fait de leur mobilité accrue et de l'ouverture plus importante de leur bouche, les juvéniles sont plus à même de capturer aisément les proies les plus énergétiques (Nunn *et al.,* 2007b; Bison *et al.,* 2015). Les larves, moins compétitives que les juvéniles, sont alors potentiellement contraintes de consommer des ressources plus faiblement caloriques (comme les végétaux aquatiques), ce qui peut impacter leur vitesse de croissance mais également leurs chances de survie (Post & Parkinson, 2001). Néanmoins, bien que la raréfaction des ressources puisse augmenter la mortalité au sein d'une population, ce phénomène est rarement observé en milieu naturel car la compétition trophique force généralement les individus à partitionner leur régime alimentaire (Olsson *et al.,* 2006; Bolnick *et al.,* 2010; Araújo *et al.,* 2011). La régulation de la Meuse a induit une spécialisation individuelle chez les alevins les plus soumis à la compétition alimentaire, uniquement sur le site navigable où les ressources sont potentiellement moins diversifiées et accessibles. Les jeunes individus sur la station faiblement aménagée ont plutôt un régime généraliste centré sur les macroinvertébrés tandis que certains individus sur la station navigable ne consomment qu'un type de proies bien déterminé comme les chironomidae, les bryophytes, les algues…. Cette spécialisation alimentaire pourrait être un moyen pour les individus les moins compétitifs de pallier le manque de zooplancton et de réduire la concurrence portant sur les macroinvertébrés benthiques. La compétition alimentaire ne semble toutefois pas directement impacter la survie des larves, mais pourrait avoir des conséquences indirectes. La faible croissance des individus consommant les proies les moins énergétiques pendant la saison estivale pourrait induire une mortalité plus élevée pendant la période hivernale, les larves de petite taille ayant un taux de survie plus faible lors des épisodes froids (Hurst & Conover, 1998). Néanmoins, à notre connaissance, aucune étude n'a mis en évidence l'influence directe des activités anthropiques, comme l'eutrophisation ou les aménagements de cours d'eau, sur la spécialisation alimentaire individuelle. La diversité des interactions trophiques ainsi que leurs influences mutuelles complexifient les études trophiques et limitent le développement de liens de causalité avec les caractéristiques du milieu même dans le cas d'écosystèmes dotés d'un faible nombre d'espèces et peu impactés par les activités humaines (Evangelista *et al*., 2014).

Les principaux résultats détaillés précédemment illustrent la forte variabilité des régimes alimentaires en fonction du stade ontogénique, de l'espèce, de l'habitat et également de l'individu (Brose *et al.,* 2006). Etudier les relations trophiques au sein d'un grand hydrosystème est trop complexe pour incriminer directement l'homogénéisation de l'habitat comme étant une limite au recrutement de certaines espèces omnivores en cas de raréfaction

des ressources planctoniques. Certaines données ou actions auraient pu nous permettre d'affiner cette étude et d'apporter de nouveaux éléments de réponse à cette question. Par exemple, la capture d'un plus grand nombre d'alevins de perche européenne en France ou d'ablette commune en Belgique nous aurait permis d'évaluer l'importance du recrutement de différentes espèces, aux régimes alimentaires divergents et aux effectifs dissemblables, en fonction des caractéristiques du cours d'eau. Enfin, une alternative aux études *in situ* serait la mise en place de vastes expériences en milieu contrôlé permettant d'élargir nos perspectives d'études et de quantifier de manière plus précise les échanges de matières entre les différents compartiments. Il serait pertinent de comparer en rivière artificielle, le taux de survie, la croissance, le régime alimentaire ainsi que la compétition trophique des alevins en fonction de la diversification de l'habitat et de l'abondance des ressources planctoniques. Toutefois, recréer des mésocosmes complexes composés de plusieurs niveaux trophiques (pythoplancton, zooplancton, macroinvertébré et poisson) nécessiterait des infrastructures extérieures coûteuses et la difficulté de maintenir des larves de poissons en milieu contrôlé réduirait, de manière importante, les chances de réussite de pareille entreprise.

3. Conclusions

Ce ne sont ni les résultats obtenus, ni les méthodes statistiques ou analytiques employées au cours des chapitres précédents qui font l'originalité de ce travail mais bel et bien l'étude conjointe des niches fonctionnelles théoriques et observées des communautés. La prise en compte de ces descripteurs nous a permis d'appréhender une série de tendances crédibles sur un écosystème particulièrement complexe à étudier du fait des multiples pressions dont il fait l'usage. L'analyse à long terme de la Meuse révèle que les communautés de macroinvertébrés benthiques et de poissons suivent les mêmes tendances que dans la plupart des grands fleuves anthropisés, favorisant les espèces prolifiques au détriment des taxons plus exigeants. Cependant, l'origine de cette évolution sur la Meuse ne serait pas attribuée au réchauffement global comme explicité par la majorité des études de ces dernières années (Hughes, 2000; Daufresne & Boët, 2007; Daufresne *et al.*, 2007; Buisson *et al.*, 2008; Floury *et al.*, 2013; Piggott *et al.*, 2015) mais serait en partie liée à des interactions trophiques engendrées par des taxons exogènes. Cette divergence pourrait être due à la qualité des données compulsées lors de notre recherche, à l'histoire particulière du fleuve ou à la prise en compte de certains facteurs d'ordre biologique potentiellement confondants. L'identification des causes influençant directement ou indirectement les communautés constitue pourtant un enjeu majeur pour les scientifiques et les gestionnaires de cours d'eau dans l'identification des principaux facteurs de perturbations. Il est donc particulièrement essentiel que la communauté scientifique pérennise et partage les suivis écologiques à long terme et propose de nouvelles approches statistiques multifactorielles, permettant de mieux identifier les relations causales qui sont en jeu au sein de l'écosystème.

L'approche fonctionnelle des assemblages de macroinvertébrés et de poissons a permis de mesurer l'influence de la qualité physique de l'habitat et, plus précisément, de la régulation des cours d'eau sur la structure et la résilience des communautés. La chenalisation de la

Meuse semble appliquer un filtre sur certains traits biologiques ou écologiques limitant diverses stratégies fonctionnelles. Contrairement à la Meuse française, la diminution des apports en matières azotées et phosphorées n'a pas bénéficié aux espèces plus exigeantes en Meuse belge manifestement du fait de l'absence d'habitats suffisamment sains ou diversifiés. Néanmoins, en dépit des données mises à contribution et des multiples inventaires réalisés, nous n'avons pu identifier l'influence de l'aménagement de l'habitat dans le fonctionnement trophique des communautés dulcicoles. Deux raisons majeures semblent être à l'origine de ce constat. La première résulte de l'analyse isotopique des matières carbonées consommées par les communautés. En cas de faible abondance de ressources planctoniques, les principaux apports carbonés proviennent majoritairement de la végétation riveraine et de la végétation aquatique (algues et bryophytes) indépendamment du niveau de rectification de la Meuse. Contrairement à la théorie du « River Continuum Concept » (Vannote *et al.*, 1980), le periphyton n'est pas ou peu consommé, aussi bien dans la zone dite « à barbeau » que dans la zone « à brème » de la Meuse. Cette théorie apparait alors trop simpliste pour les fleuves soumis à de multiples pressions et tend à être remplacée par des concepts plus complexes incluant la variabilité temporelle des caractéristiques d'habitats notamment induite par des changements de débits (Thorp & Bowes, 2017) comme le « River habitat Templet » (Townsend & Hildrew, 1994) et ses adaptations (Riverine Productivity Model; Thorp & Delong, 2002). La seconde provient de notre étude sur la compétition trophique des alevins de la Meuse belge et française. En absence de zooplancton, les alevins des deux biefs étudiés ont un régime alimentaire relativement identique aux individus plus âgés induisant ainsi une spécialisation alimentaire plus marquée au niveau de la station belge, avec une partie de la population consommant des aliments peu énergétiques. Toutefois, cette concurrence ne semble pas impacter la survie des alevins pendant la saison estivale mais pourrait, en revanche, augmenter la mortalité des jeunes individus de plus faible taille au cours de la période hivernale, réduisant ainsi le recrutement des adultes.

Si certaines de nos hypothèses sont restées sans réponse, nous avons pu tout de même mettre en avant le rôle essentiel de l'habitat dans le maintien de la biodiversité et de la dynamique du système. La gestion hydraulique française de la Meuse, peu intrusive, a permis à certaines espèces de profiter de l'amélioration de la qualité physico-chimique de la rivière mais a également maintenu une communauté ichtyologique abondante malgré la décroissance du plancton. La chenalisation des rivières et l'homogénéisation des habitats ont eu un effet particulièrement délétère sur le fonctionnement des communautés et sur la résilience du système (Scheffer & Carpenter, 2003) qui ne peut qu'être renforcé par les différentes activités humaines et les changements globaux (Travis, 2003). Ce constat plaide pour la mise en place de mesures de renaturation de cours d'eau qui permettraient à la faune de réintégrer un biotope leur offrant toutes les caractéristiques nécessaires à leur développement, tout en maintenant les activités humaines, et répondraient à certains enjeux communautaires définis par la DCE.

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Annexes

Appendix 1: Biological and ecological traits and their categories describing the biological adaptations and ecological preferences of benthic macroinvertebrates based on Tachet et al. (2010). Codes of categories and groups were used as labels in App. 4. A GAM trend tests was applied on each trait-categories (* P < 0.05, ** P < 0.01, *** P < 0.001).

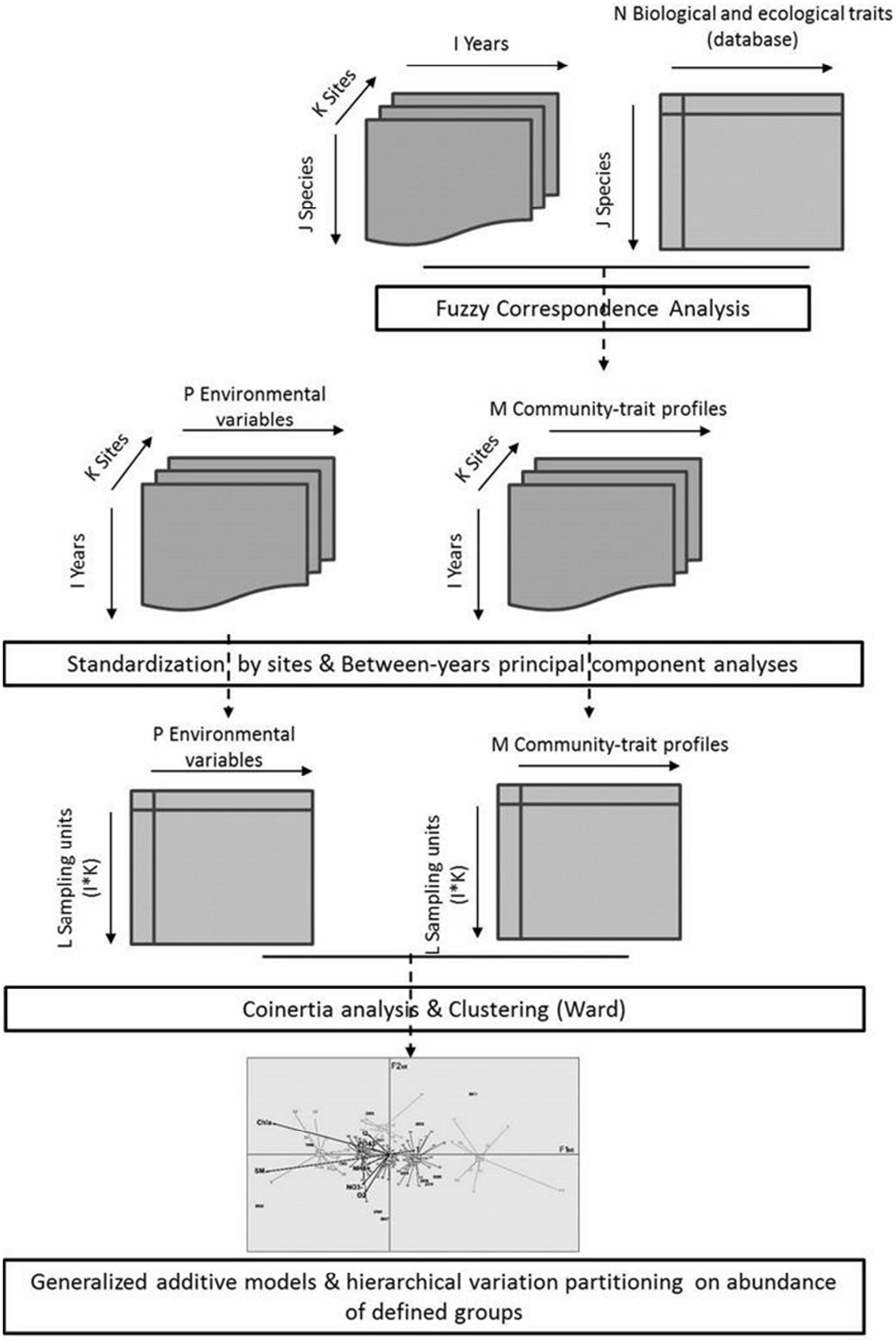
Trait	Trait categories	Code	Group	Trend	R^2 adj
Maximal potential size (cm)	Inf 0.25	1	4	-	0
	Between 0.25-0.5	2	6	↗	**0.16***
	Between 0.5-1	3	6	-	0
	Between 1-2	4	1	-	0.08
	Between 2-4	5	3	-	0.05
	Between 4-8	6	2	↘	**0.25****
	Sup 8	7	2	↘	**0.24****
Life cycle duration	< 1 year	8	6	-	**0.21****
	1 year	9	1	-	0.12
	> 1 year	10	1	-	**0.16***
Potential number of cycles per year	≤ 1	11	5	-	0
	> 1 year	12	5	-	0
Aquatic stages	egg	13	5	-	0
	larva	14	2	-	0.07
	nymph	15	3	-	0.03
	adult	16	5	-	0
Reproduction	ovoviviparity	17	6	-	0
	isolated eggs free	18	4	-	0
	isolated eggs cemented	19	1	-	0
	clutches cemented or fixed	20	6	-	0.06
	clutches free	21	1	↘	**0.24****
	clutches in vegetation	22	2	-	0
	clutches terrestrial	23	4	-	0.003
	asexual reproduction	24	2	-	0.03
Dispersal	aquatic passive	25	2	-	0
	aquatic active	26	3	↘	**0.18****
	aerial passive	27	5	-	0
	aerial active	28	5	-	0
Resistance forms	eggs statoblasts	29	4	-	0.009
	cocoons	30	1	↘	**0.15***
	housings against desiccation	31	4	↗	**0.16***
	diapause or dormancy	32	5	-	0
	none	33	3	-	0
Respiration	tegument	34	1	-	0.09
	gill	35	5	-	0
	plastron	36	4	-	0
	spiracle	37	5	-	0
	hydrostatic vesicle	38	4	-	0.06
Locomotion and substrate relation	flier	39	4	-	0
	surface swimmer	40	5	-	0
	full water swimmer	41	5	-	0
	crawler	42	5	-	0
	burrower	43	4	-	0
	interstitial	44	1	↘	**0.25****
	temporarily attached	45	3	-	0.09
	permanently attached	46	3	-	0
Food	microorganisms	47	4	↘	**0.18***
	detritus	48	4	-	0
	dead plant	49	3	-	0
	living microphytes	50	5	-	0
	living macrophytes	51	6	↗	**0.50*****
	dead animal	52	2	↘	**0.16****
	living microinvertebrates	53	3	↘	**0.16****
	living macroinvertebrates	54	1	↘	**0.19****
	vertebrates	55	4	-	0

Trait	Trait categories	Code	Group	Trend	R^2 adj
Feeding habits	absorber	56	4	-	0
	deposit feeder	57	2	↘	**0.16****
	shredder	58	5	-	0
	scraper	59	6	↗	**0.18****
	filter feeder	60	3	-	0
	piercer	61	5	-	0
	predator	62	1	↘	**0.42*****
	parasite	63	4	-	0
Transversal distribution	river channel	64	5	-	0
	banks connected side arms	65	5	-	0
	ponds pools disconnected side arms	66	2	-	0
	marshes peat bogs	67	4	-	0
	temporary waters	68	4	↘	**0.17***
	lakes	69	2	↘	**0.16***
	groundwaters	70	4	-	0.02
Longitudinal distribution	crenon	71	2	↘	**0.21****
	epirithron	72	2	↘	**0.27****
	metarithron	73	2	↘	**0.16***
	hyporithron	74	2	↘	**0.16***
	epipotamon	75	5	↗	**0.19***
	metapotamon	76	5	-	0.03
	estuary	77	5	-	0
	outside river system	78	5	-	0
Altitude	lowlands	79	5	↗	**0.14***
	piedmont level	80	2	-	0
	alpine level	81	4	-	0.05
Substrate (preferendum)	flags boulders cobbles pebbles	82	3	-	0
	gravel	83	4	-	0
	sand	84	5	-	0
	silt	85	4	-	0
	macrophytes	86	4	-	0
	microphytes	87	4	-	0
	twigs roots	88	3	↘	**0.31*****
	organic detritus litter	89	2	-	0
	mud	90	4	-	0
Current velocity (preferendum)	null	91	5	-	0
	slow	92	5	-	0
	medium	93	2	-	0
	fast	94	2	-	0
Trophic status (preferendum)	oligotrophic	95	1	-	0
	mesotrophic	96	4	-	0.06
	eutrophic	97	6	-	0.03
Salinity (preferendum)	freshwater	98	1	-	0.02
	brackish water	99	6	↗	**0.16***
Temperature	cold (< 15C)	100	2	↘	**0.61*****
	warm (> 15C)	101	5	↗	**0.12***
	eurythermic	102	5	-	0.05
Saprobity	xenosaprobic	103	2	-	0.03
	oligosaprobic	104	3	↘	**0.21****
	β mesosaprobic	105	4	-	0
	α mesosaprobic	106	5	-	0.03
	polysaprobic	107	5	-	0.04
pH (preferendum)	< 4	108	2	↘	**0.63*****
	Between 4-4.5	109	2	↘	**0.51*****
	Between 4.5-5	110	2	↘	**0.46*****
	Between 5-5.5	111	1	↘	**0.37*****
	Between 5.5-6	112	2	↘	**0.3****
	> 6	113	6	↗	**0.53*****

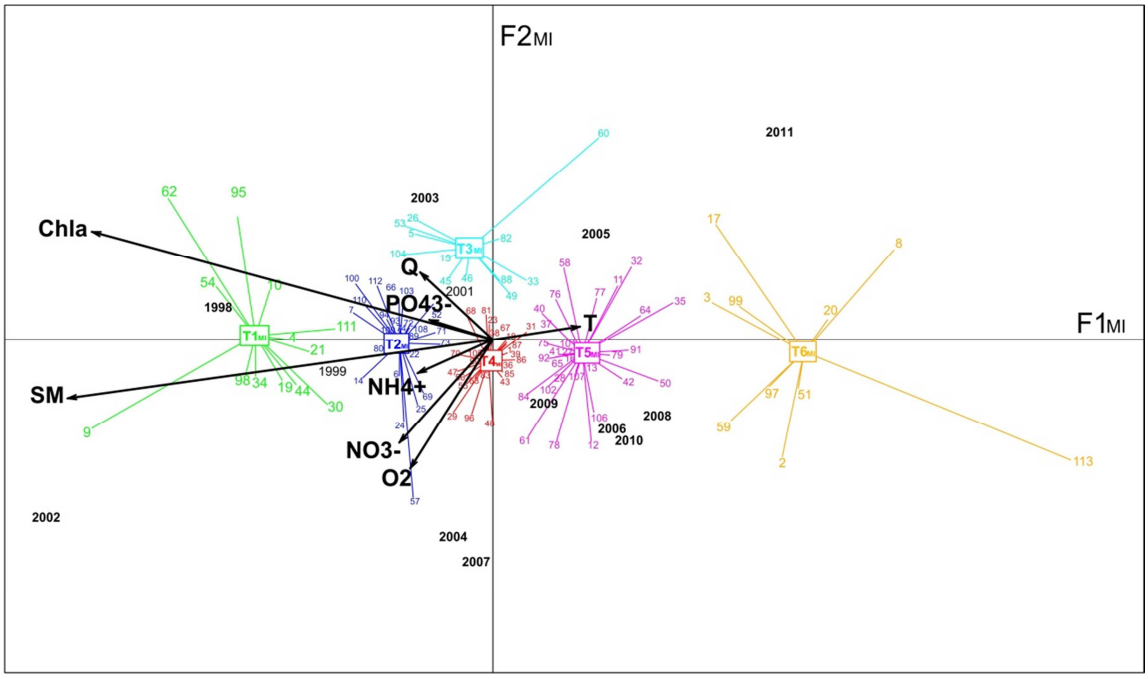
Appendix 2: Biological and ecological traits and their categories describing fish biological adaptations and ecological preferences based on Blanck and colleagues (2007). Codes of categories and groups were used as labels in App.5. A GAM trend tests was applied on each trait-categories (* P < 0.05, ** P < 0.01, *** P < 0.001).

Trait	Trait categories	Code	Group	Trend	R^2 adj
adult body length (cm)	< 10	1	3	↗	**0.10***
	≥10-20	2	3	-	0.03
	≥20-40	3	1	↘	**0.36****
	≥ 40	4	2	-	0
reproduction habitat	phytophilic	5	1	-	0
	lithophilic	6	3	-	0
	phyto-lithophilic	7	2	-	0
	psammophilic	8	2	-	0.04
relative fecundity (number of oocytes / g)	<57	9	2	-	0.06
	≥57-200	10	2	-	0
	≥ 200	11	2	-	0.01
number of spawning events / year	≤ 1	12	1	↘	**0.62*****
	> 1	13	3	↗	**0.62*****
egg diameter (mm)	< 1.35	14	2	-	0
	≥1.35-2	15	2	-	0
	≥ 2	16	2	-	0
age at first maturity (year)	1	17	2	↗	**0.11***
	2	18	3	-	0
	3	19	1	↘	**0.38****
	4	20	2	-	0
	5	21	2	-	0
parental care	no protection	22	2	-	0.08
	protection with nesters	23	2	-	0.07
	no protection with nesters	24	2	-	0
feeding habitat	benthivorous	25	2	-	0.07
	water column	26	2	-	0.07
feeding diet	invertebrate feeders	27	3	↗	**0.41*****
	piscivorous	28	2	-	0.07
	omnivorous	29	1	↘	**0.47*****
	carnivorous	30	2	-	0
rheophily habitat	rheophilic	31	3	-	0
	limnotopic	32	1	-	0
	eurytopic	33	2	-	0
habitat preference	pelagic	34	2	-	0.09
	benthopelagic	35	2	-	0
	demersal	36	2	-	0

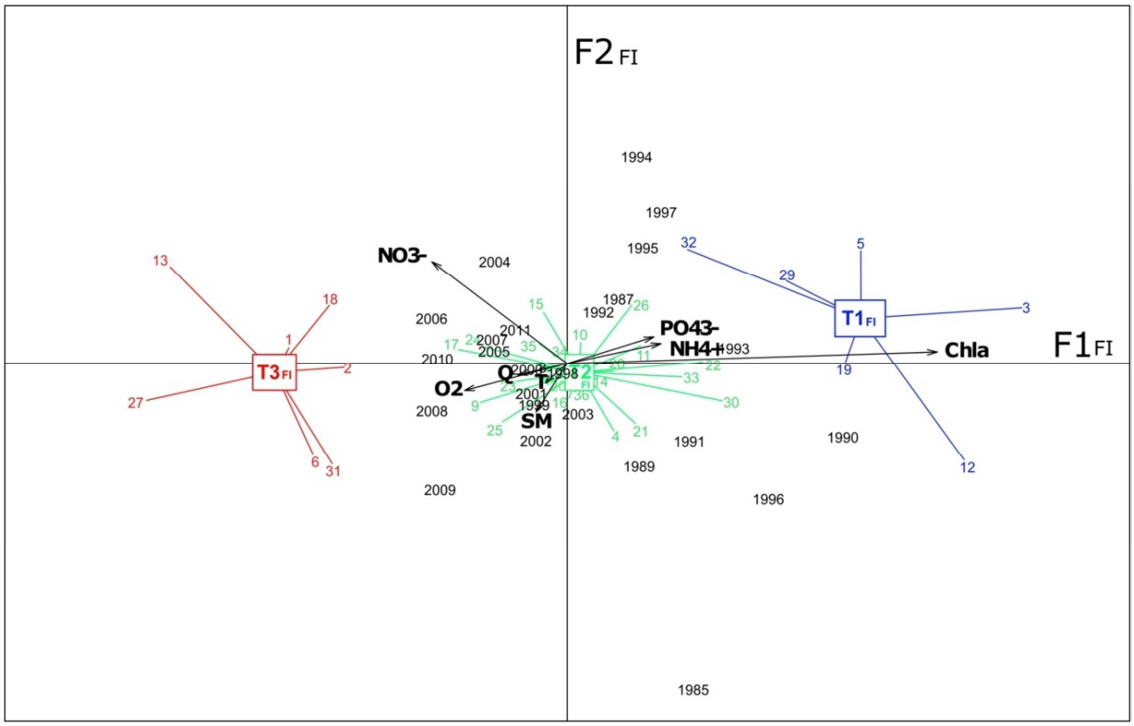
Appendix 3: Statistical methodology schematic summary



Appendix 4: Results of the co-inertia analysis matching the information on macroinvertebrate trait category frequencies and physico-chemical characteristics of the river Meuse over the 1998-2010 period. Data were previously centered "by-site" to reduce the effect of river typology. "Between-years" PCA (bPCA) was preliminarily applied to each data array. Each year is located on the first factorial plane according to the mean physico-chemical and macroinvertebrate assemblage trait characteristics of sites at the selected sampling date. The six macroinvertebrate groups ($T1_{MI}$ to $T6_{MI}$) were defined by hierarchical cluster analysis (Ward algorithm) on the Euclidean distance matrix calculated according to their F1 and F2 scores in CoI. Each trait category was included in a group gathering trait categories following the same trend pattern over the study period. The location of each group of trait category is at the weighted average of the locations of individual trait categories belonging to this group. Each trait category is linked to the mean location of the corresponding group by a line. The full labels of invertebrate trait categories (codes 1-113) are in Appendix 1. See the text for further details.



Appendix 5: Results of the co-inertia analysis g matching the information on fish-trait category frequencies and physico-chemical characteristics of the river Meuse over the 1985-2010 period. Data were previously centred "by-site" to reduce the effect of river typology."Between-years" PCA (bPCA) was preliminarily applied to each data array. Each year is located on the first factorial plane according to the mean physico-chemical and fish assemblage trait characteristics of sites at the selected sampling date. The three fish groups ($T1_{FI}$ to $T3_{FI}$) were defined by hierarchical cluster analysis (Ward algorithm) on the Euclidean distance matrix calculated according to their F1 and F2 scores in CoI. Each trait category was included in a group gathering trait categories following the same trend pattern over the study period. The location of each group of trait category is at the weighted average of the locations of individual trait categories belonging to this group. Each trait category is linked to the mean location of the corresponding group by a line. The full labels of fish trait categories (codes 1-36) are in Appendix 2.See the text for further details.



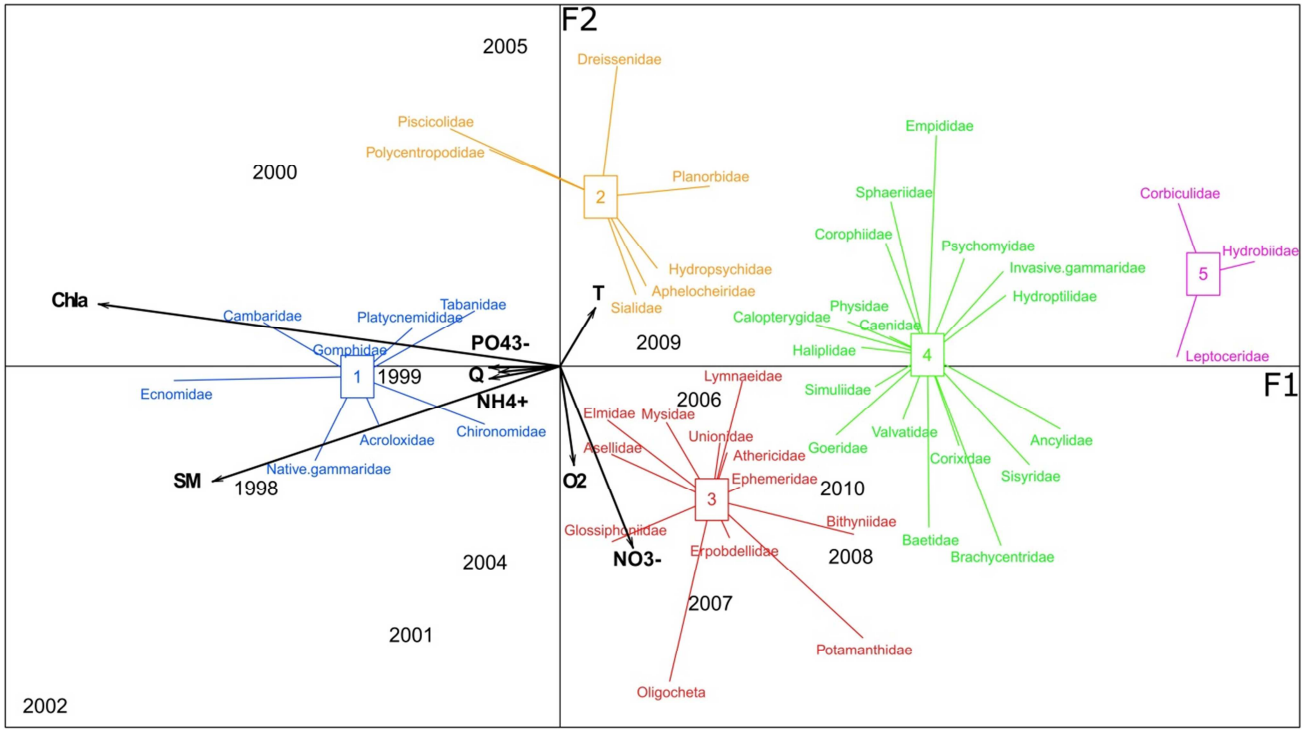
Appendix 6: Macro-invertebrate data of the French River Meuse from 1998 to 2011 at Sassey sur Meuse

Appendix 6 may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1621/full

Appendix 7: Fish data of the French River Meuse from 1985 to 2010 at Han sur Meuse (S1), Sassey sur Meuse (S2) and Ham sur Meuse (S3)

Appendix 7 may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1621/full

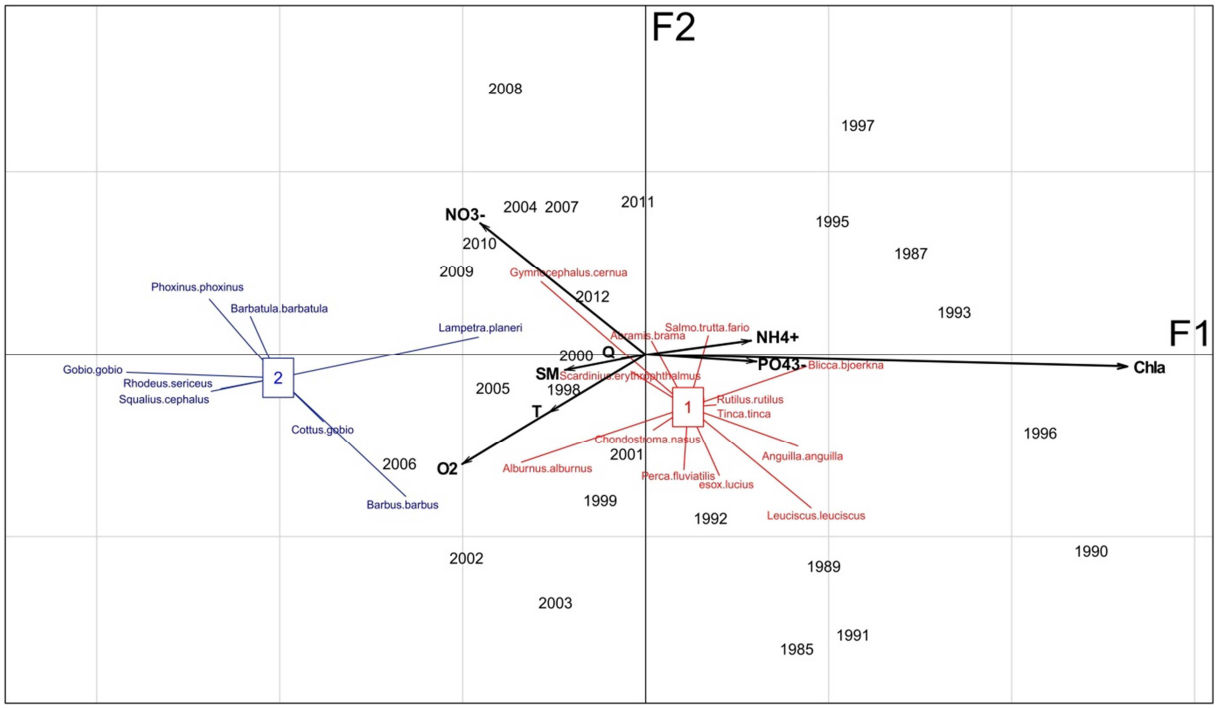
Appendix 8: Results of the co-inertia analysis matching the information on macroinvertebrate abundances and physico-chemical characteristics of the river Meuse over the 1998-2010 period (RV : 0,66). Data were previously centered “by-site” to reduce the effect of river typology. “Between-years” PCA (bPCA) was preliminarily applied to each data array. The five macroinvertebrate groups were defined by hierarchical cluster analysis (Ward algorithm) on the Euclidean distance matrix calculated according to their F1 and F2 scores in CoI. (F1 : 77,2% and F2 : 16,5%).



Appendix 9: Results of the MK-trend tests applied to the abundances of five macroinvertebrate groups in the Meuse River over the 1998-2010 period. Independent contributions of physical and chemical parameters to variations in the abundances of macroinvertebrate group value variations over the study period are provided. (*P < 0.05, ** P < 0.01, *** P < 0.001).

	MK trend test		Hierarchical variation partitioning						MK trend test		Hierarchical variation partitioning						MK trend test		Hierarchical variation partitioning				
	Trend	Pt	Variable	I	*Pi*	R²	*P*		Trend	Pt	Variable	I	*Pi*	R²	*P*		Trend	Pt	Variable	I	*Pi*	R²	*P*
			Chla	26.7	**0.024**	54.1	**<0.001**				Chla	10.3	0.394	7.3	0.523				Chla	7.1	0.444	16.3	0.11
			NH_4^+	2.3	0.778	3.9	0.653				NH_4^+	10.3	0.361	9.5	0.399				NH_4^+	14.8	0.124	8.2	0.425
			NO_3^-	2.9	0.713	2.7	0.689				NO_3^-	31.6	**0.002**	45	**<0.001**				NO_3^-	8.1	0.514	19.1	0.178
Group 1	–	**0.002**	PO_4^{3-}	10.8	0.308	3.3	0.647	**Group 2**		0.228	PO_4^{3-}	3.2	0.719	1.5	0.711	**Group 3**		0.913	PO_4^{3-}	3.5	0.704	0.4	0.763
			O_2	2.5	0.73	5.9	0.564				O_2	4.5	0.648	11.2	0.4				O_2	32.3	**<0.001**	43.5	**<0.001**
			Q	3.9	0.698	8.9	0.499				Q	10.3	0.38	0.1	0.781				Q	3.2	0.709	9.1	0.462
			T	13	0.181	20.3	0.085				T	2.6	0.729	0	0.797				T	1.9	0.754	2.9	0.667
			SM	15.8	0.114	38.1	**0.001**				SM	16.8	0.054	23.7	**0.028**				SM	6.5	0.588	5.4	0.61
			Chla	32	**0.002**	58.5	**<0.001**				Chla	21.3	0.075	38.6	**<0.001**								
			NH_4^+	6.5	0.531	15.3	0.193				NH_4^+	5.3	0.607	13.9	0.293								
			NO_3^-	3.7	0.674	0.4	0.771				NO_3^-	4.4	0.643	1.4	0.691								
Group 4	↗	**<0.001**	PO_4^{3-}	4.1	0.608	2.7	0.674	**Group 5**	↗	**0.001**	PO_4^{3-}	11.5	0.331	14.1	0.228								
			O_2	0.6	0.746	1.3	0.703				O_2	0.5	0.825	0.1	0.785								
			Q	2.6	0.757	5	0.63				Q	2.7	0.736	0	0.822								
			T	4.9	0.643	9.6	0.469				T	4.2	0.68	3.5	0.673								
			SM	35.9	**<0.001**	67.2	**<0.001**				SM	46.8	**<0.001**	73.6	**<0.001**								

Appendix 10: Results of the co-inertia analysis matching the information on fish abundances and physico-chemical characteristics of the river Meuse over the 1985-2010 period (RV : 0,30). Data were previously centered “by-site” to reduce the effect of river typology. “Between-years” PCA (bPCA) was preliminarily applied to each data array. The two fish were defined by hierarchical cluster analysis (Ward algorithm) on the Euclidean distance matrix calculated according to their F1 and F2 scores in CoI. (F1 : 83,0% and F2 : 14,1%).



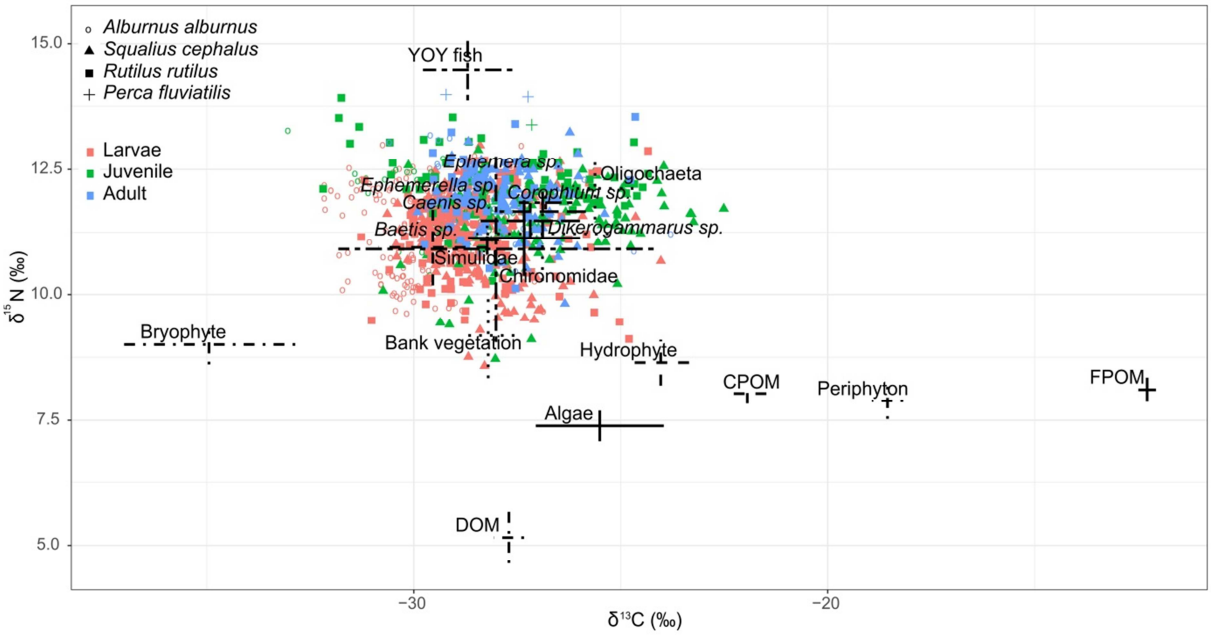
Appendix 11: Results of the MK-trend tests applied to the abundances of two fish groups in the Meuse River over the 1985-2010 period. Independent contributions of physical and chemical parameters to variations in the abundances of fish group value variations over the study period are provided. (*P < 0.05, ** P < 0.01, *** P < 0.001).

	MK trend test		Hierarchical variation partitioning						MK trend test		Hierarchical variation partitioning				
	Trend	Pτ	Variable	I	*Pi*	R^2	*P*		Trend	Pτ	Variable	I	*Pi*	R^2	*P*
Group 1		0.944	Chla	1.5	0.685	0.1	0.761	**Group 2**	↗	**<0.001**	Chla	26.6	**<0.001**	44.8	**<0.001**
			NH_4^+	7	0.281	5.6	0.414				NH_4^+	8.5	0.215	11.9	0.083
			NO_3^-	0.8	0.744	0.1	0.777				NO_3^-	3.2	0.561	8.1	0.24
			PO_4^{3-}	12.4	**0.038**	15.4	**0.017**				PO_4^{3-}	2.5	0.643	5.2	0.47
			O_2	18.4	**<0.001**	36.1	**<0.001**				O_2	4.5	0.459	0.7	0.659
			Q	8.4	0.288	20	**0.008**				Q	1.3	0.702	0.6	0.724
			T	18.6	**0.002**	11.6	0.074				T	20.3	**0.007**	43.2	**<0.001**
			SM	0.5	0.778	0	0.789				SM	0.8	0.737	0.7	0.725

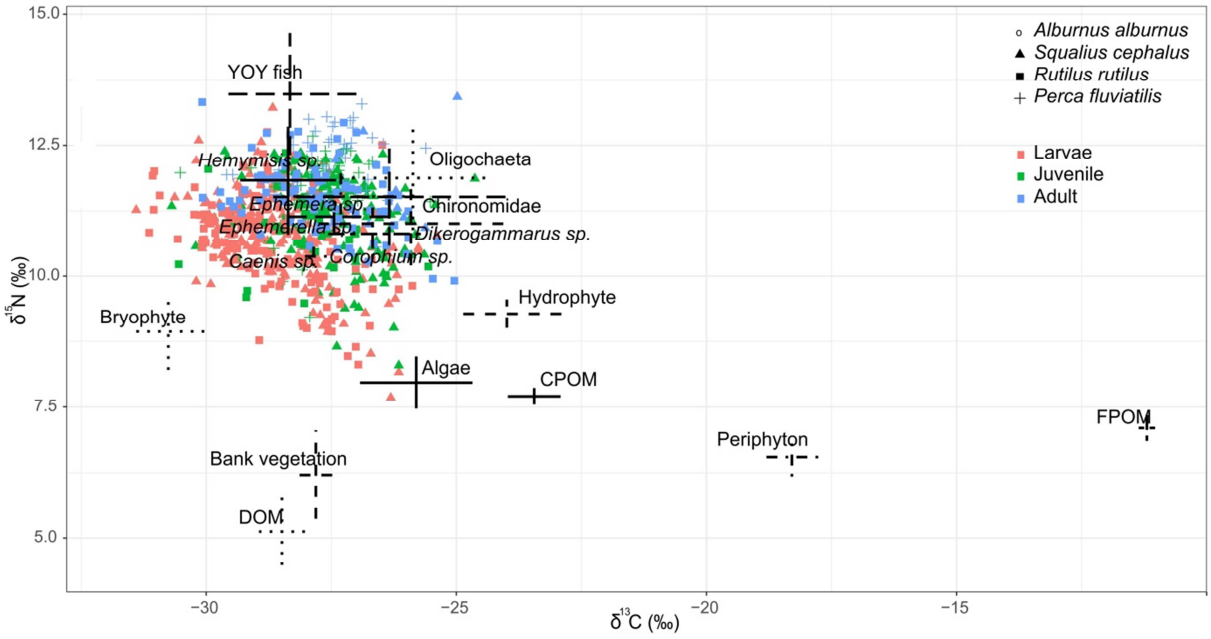
Appendix 12: Mean $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values, sample number and estimated standard ellipse area (SEA_C) of consumers and potential sources sampled in the Meuse River at Ham-sur-Meuse between 2013 and 2014. (DOM: detrital organic matter, FPOM: fine particulate organic matter (0.6 - 30 µm), CPOM: coarse particulate organic matter (30 - 100 µm), Macroinvertebrate IR: herbivorous benthic macroinvertebrates, Macroinvertebrate IIR: predator benthic macroinvertebrates, YOY fish: young of the year fish sampled in the whole community).

		Ham sur Meuse				Waulsort			
		$\delta^{13}C \pm SD$	$\delta^{15}N \pm SD$	N	SEAc	$\delta^{13}C \pm SD$	$\delta^{15}N \pm SD$	N	SEAc
Common bleak	Larvae	-29.9 ± 0.8	11.2 ± 0.4	129	1.9	-28.8 ± 0.4	11.6 ± 0.2	9	1.3
Chub		-28.5 ± 1.1	11.1 ± 0.7	167	2.8	-28.5 ± 1.0	10.8 ± 0.8	163	2.8
Roach		-28.7 ± 0.7	11.3 ± 0.8	185	2.5	-28.7 ± 0.8	10.8 ± 0.6	176	2.4
Common bleak	Juvenile	-29.4 ± 0.4	11.8 ± 0.3	46	1.4			0	
Chub		-27.1 ± 1.4	11.4 ± 0.8	125	2.4	-27.3 ± 0.9	11.1 ± 0.6	104	2.9
Roach		-27.7 ± 1.0	12.3 ± 0.4	84	2.2	-28.0 ± 0.7	10.8 ± 0.7	54	1.9
European perch		-27.9 ± 0.6	11.9 ± 0.2	5	0.7	-27.8 ± 0.7	11.7 ± 0.7	54	1.5
Common bleak	Adult	-28.2 ± 0.6	11.9 ± 0.6	30	2.7			0	
Chub		-27.4 ± 0.7	11.9 ± 0.9	67	1.7	-26.3 ± 0.7	11.7 ± 0.9	9	2.2
Roach		-28.3 ± 0.9	12 ± 0.7	65	1.8	-27.7 ± 1.1	11.5 ± 0.6	88	2.1
European perch		-27.87 ± 0.4	13.1 ± 0.4	3	1.5	-27.5 ± 0.8	12.3 ± 0.6	38	1.5
Algae		-26.6 ± 1.5	4.9 ± 0.3	12		-26.9 ± 1.1	5.5 ± 0.5	13	
Bryophyte		-36.2 ± 2.0	7.5 ± 0.4	5		-32.7 ± 0.7	7.1± 0.7	2	
Hydrophyte		-24.9 ± 0.7	6.8 ± 0.4	9		-24.8 ± 1.1	7.4 ± 0.2	7	
DOM		-29.1 ± 0.4	1.6 ± 0.5	17		-29.9 ± 0.4	1.5 ± 0.6	13	
Periphyton		-18.7 ± 0.4	5.2 ± 0.2	32		-18.5 ± 0.5	3.9 ± 0.2	28	
FPOM		-11.6 ± 0.2	5.6 ± 0.1	32		-10.5 ± 0.1	4.6 ± 0.1	82	
CPOM		-22.7 ± 0.4	5.7 ± 0.2	25		-24.2 ± 0.5	5.4 ± 0.1	14	
Bank vegetation		-29.6 ± 0.6	6.7 ± 0.5	11		-29.2 ± 0.3	3.8 ± 0.5	25	
Macroinvertebrates IR		-30.5 ± 1.9	7.3 ± 0.9	54		-29.9 ± 1.6	7.1 ± 0.6	55	
Macroinvertebrates IIR		-29.5 ± 1.4	8.5 ± 0.9	80		-28.9 ± 1.8	8.2 ± 0.7	53	
YOY fish		-30.2 ± 1.0	11.9 ± 0.6	51		-29.8 ± 1.3	10.9 ± 1.1	29	

Appendix 13: $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values of the 4 fish studied species sampled in the Meuse River at Ham-sur-Meuse between 2013 and 2014. Symbols represent individual isotopic values for of each fish species, grouped by ontogenic stage (color). Mean value and standard deviations of potential food sources are represented by black dashed lines (DOM: detrital organic matter, FPOM: fine particulate organic matter, CPOM: coarse particulate organic matter). For consumers, the trophic enrichment factor was added to the mean $\delta^{15}N$.



Appendix 14: $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values of the 4 fish species sampled in the Meuse River at Waulsort between 2013 and 2014. Symbols represent individual isotopic isotopic values for of each fish species, grouped by ontogenic stage (color). Mean value and standard deviations of potential food sources are represented by black dashed lines (DOM: detrital organic matter, FPOM: fine particulate organic matter, CPOM: coarse particulate organic matter). For consumers, the trophic enrichment factor was added to the mean $\delta^{15}N$.



Appendix 15: Representation of the isotopic niches, built using $\delta^{13}C$ and $\delta^{15}N$ values, for 4 fish species, grouped by ontogenic stages (color), collected in the Ham-sur-Meuse and Waulsort sites of the Meuse River between 2013 and 2014. The corrected standard ellipse area (SEA_C) comprises 40% of the sample of each group (solid lines).